PREPRINT (Version 2)

Non-avian reptile learning 40 years on: advances and promising new directions

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Word count: 27,623

Abstract

Recently, there has been a surge in cognition research using non-avian reptile systems. As a diverse group of animals, non-avian reptiles (turtles, the tuatara, crocodilians, and squamates - lizards, snakes and amphisbaenids) are good model systems for answering questions related to cognitive ecology; from the role of the environment in impacting brain, behaviour and learning, to how social and life-history factors correlate with learning ability. Furthermore, given their variable social structure and degree of sociality, studies on reptiles have demonstrated that group living is not a pre-condition for social learning. Past research has undoubtedly demonstrated that non-avian reptiles are capable of more than just instinctive reactions and basic cognition. Despite their ability to provide answers to fundamental questions in cognitive ecology, and a growing literature base, there have been no systematic syntheses of research in this group. Here, we systematically, and comprehensively review studies on reptile learning. We identify 92 new studies investigating learning in reptiles not included in previous reviews on the same topic – affording a unique opportunity to provide a more in-depth synthesis of existing work, its taxonomic distribution, the types of cognitive domains tested and methodology that has been used. Our review therefore provides a major update on our current state of knowledge and ties the collective evidence together under nine umbrella research areas: (1) habituation, (2) conditioning, (3) aversion learning, (4) spatial learning, (5) learning during foraging, (6) numerical competency, (7) learning flexibility, (8) problem solving, and (9) social learning. Importantly, we identify knowledge gaps and propose themes which offer important future research opportunities including how cognitive ability might influence fitness and survival, testing cognition in ecologically relevant situations, comparing cognition in invasive and non-invasive populations of species, and social learning. To move the field forward, it will be immensely important to build upon the descriptive approach of testing if a species can learn a task with experimental studies elucidating causal reasons for cognitive variation within and between species. With the appropriate methodology, this young but rapidly growing field of research should advance greatly in the coming years providing significant opportunities for

addressing general questions in cognitive ecology and beyond.

Keywords: Amphisbaenia, Chelonia, Crocodilia, Rhynchocephalia, Squamata, Serpentes, Sauria, cognition, integrative review

Content

I. Introduction

Cognition, the process by which animals collect, store, and use information, is integral to fitness. It is essential for finding food and shelter, avoiding predators, finding and distinguishing between conspecifics and potential mates and adapting when environmental conditions suddenly change (Shettleworth, 2010). It is therefore not surprising that there has been immense interest in understanding what drives variation in cognition (e.g. Boogert et al., 2018; Dougherty & Guillette, 2018; Volter et al., 2018), how learning and cognitive processes impact fitness (e.g. Huebner et al., 2018; Madden et al., 2018; Thornton et al., 2014) and the underlying mechanistic basis for species differences in decision making and problem solving (e.g. Lefebvre et al., 2004; Mustafar et al., 2018; Volter et al., 2018). While we have seen a surge in cognitive studies, particularly a move towards those done in the wild, there has been a clear focus on particular taxonomic groups, such as birds and mammals. Only recently, has research begun to appreciate the diversity of cognitive variation across a broader range of animal groups and moved to take a more comprehensive comparative approach.

Non-avian reptiles, from here on called reptiles (including turtles, crocodilians, tuatara and squamates - lizards, snakes and amphisbaenids), are starting to become model systems for addressing a host of questions in cognitive ecology. For example, because many squamates are egg layers it is possible to explore how early developmental environments (independent of maternal environment) impact learning. Incubation temperature affects sexual development (temperature dependent sex determination, Warner, 2010), brain morphology (e.g. Amiel et al., 2016), behaviour (e.g. Booth, 2006; Matsubara et al., 2017) and learning (e.g. Amiel et al., 2014; Dayananda & Webb, 2017; Munch et al., 2018a). Moreover, many reptiles are precocial and the juvenile brain is much more developmentally advanced at birth compared to altricial species (Charvet & Striedter, 2011; Grand, 1992) which impact learning ability at an early age (Szabo et al., 2019a). Reptiles also show individual variation in learning ability which has been linked to behavioural type, age, dominance status and sex (e.g. Carazo et al., 2014; Chung et al.,

2017; Kar et al., 2017; Noble et al., 2014). Because some reptiles have evolved early forms of sociality (While et al., 2015; Whiting & While, 2017) they have also been foundational in understanding how familiarity affects social learning ability (e.g. Munch et al., 2018b; Whiting et al., 2018).

Phylogenetically, reptiles (including birds) split from mammals about 320 million years ago and about 280 million years ago, the reptiles diverged into two clades: archosaurs (birds and crocodiles) and lepidosaurs (tuatara and squamates [lizards, amphisbaenids, snakes])(Alföldi et al., 2011). The position of turtles was long unclear but they are now considered a sister group to lepidosaurs (Güntürkün et al., 2017). The phylogenetic relationship reptiles have to mammals and birds makes them extremely interesting models to investigate the convergent evolution of cognitive ability such as sex-differences in spatial learning (e.g. Carazo et al., 2014). Furthermore, modern reptiles are the third most speciose group of vertebrates (11,136 species as of December 2019; Uetz et al., 2019) inhabiting a wide range of different habitats, showing diversity in mating systems (monogamy to polygynandry), feeding ecology, social organisation (solitary to groups of many individuals), reproductive tactics (parthenogenesis, oviparity or viviparity) and differ substantially in behaviour (Fox et al., 2003; Reilly et al., 2009; Uller & Olsson, 2008; Whiting & While, 2017). As such, a diversity of questions regarding mechanisms underlying cognitive performance might be asked using reptile models and consequently we have seen a surge in work on reptile cognition (Figure 1) given their potential to address fundamental questions in cognitive ecology.

Gordon Burghardt (1977) conducted the first major review on reptilian cognition as the field was only just developing. His review was critical in establishing and describing methods in the field and providing an in depth overview of reptile learning. Burghardt's review included over 70 species and described learning processes from simple habituation to different forms of conditioning, maze and detour learning, and visual discrimination learning (including reversals) highlighting major limitations of existing cognitive work at the time. Suboski (1992) then sought to better understand reptilian (and amphibian) learning

through his “releaser-induced recognition learning” model. In this context, he reviewed any form of conditioning, aversion learning and recognition in reptiles (and amphibians). More recently, Wilkinson and Huber (2012) provided a small update on new developments including studies focusing on social learning – a novel direction in the study of reptilian cognition at the time. Finally, Burghardt (2013) himself wrote an update highlighting the empirical evidence supporting the diverse capabilities (cognitive and behavioural) of reptiles and the need for greater consideration of their welfare in captivity. While these have been important reviews, the explosion of recent research requires a more systematic approach to collating, reviewing and evaluating our current state of knowledge to provide a representation of our current understanding of the field.

Here, we performed the first systematic review of cognition research (primarily learning) on non-avian reptiles conducted over the last 40 years. Contrary to conventional reviews, a systematic review uses standardized and transparent search methods to select relevant studies to be included in the review (Stevens, 2001 cited by McGowan & Sampson, 2005; Higgins & Green, 2011). Multiple databases are searched and all articles are screened for relevance and inclusion based on well-defined criteria, making it less likely to miss important research and reducing biased representation of existing work. Our aim was to present a detailed overview of the learning research done in reptiles since Burghardt (1977; 2013), Suboski (1992) and Wilkinson and Huber’s (2012) updates. Importantly, we identify 118 new studies on reptile learning of which none were included in Burghardt (1977) and 26 were included in the updates (Burghardt 2013; Suboski, 1992; Wilkinson & Huber, 2012). We wanted our review to be thorough and as comprehensive as possible, functioning as a guide that will enhance future work and identify critical gaps requiring further attention and hopefully inspiring novel research questions in animal cognition, comparative psychology and cognitive ecology.

II. Systematic Review and Literature Compilation

We searched Web of Knowledge, Scopus, ProQuest Dissertation & Theses Global, Papers Library, GoogleScholar, PubMed and ScienceDirect for publications on learning (using the keywords ‘learning’, ‘cognition’, ‘behaviour’, ‘choice’ and ‘discrimination’) conducted in any non-avian reptile species (using the keyword ‘reptile’). To focus our search on relevant publications only, we excluded publications based on the keywords ‘bird’, ‘mammal’, ‘fish’, ‘fossil’, ‘parasite’, ‘frog’, ‘insect’, ‘morph’ and ‘chemi’ (for all keywords we accounted for differences in spelling). The initial search was conducted to collect data for a specific meta-analysis on sex-dependent learning (Szabo et al., 2019c); however, an additional search in Web of Science was conducted in 2019 to include more recent publications (until May 2019).

We identified a total of 35,533 records (initial search: 35,210, recent search: 232 records) of which 1,741 were duplicates (the recent search did not produce duplicates) and 208 articles were selected based on title screened for words and/ or expressions indicating a learning experiment was conducted. From these 208 articles we conducted a backward literature search of their references which produced an additional 92 records (82 original works, 10 reviews) and a forward search (citations to these articles) identifying a further 38 records (36 original studies and 2 reviews) to affirm completeness of the initial searches. We then screened the abstracts of the 337 (208 initially found plus 92 from the backwards search and 37 from the forward search) publications for any mention of a learning experiment conducted on a non-avian reptile identifying 201 papers for full-text screening. During full-text screening we looked for a description of any learning experiment (learning task = “The acquisition of a novel behaviour, novel behaviour-sequence or novel application of existing behaviour” such as general associative learning, spatial learning, discrimination learning, avoidance learning, reinforcement learning, social or motor learning, taste aversion, habituation, conditioning, or maze learning; Shettleworth, 2010). Studies on, for example, gaze following or orientation mechanisms did not fully fit our criteria and were not included in our review.

After further scrutinizing papers based on their methods (describing a learning task

as we defined above) our final sample included 118 studies with 92 not previously identified across recent reviews. We grouped findings together under nine umbrella research areas: habituation of behaviour, animal training through operant conditioning, avoiding aversive stimuli, spatial learning and memory, learning during foraging, quality and quantity discrimination, responding to change, solving novel problems and social learning (for an overview see Figure 2 and 3) similar to previous work by Burghardt (1977), Shettleworth (2010) and Wilkinson and Huber (2012). We then grouped findings by taxon to split information into smaller chunks similar to Burghardt (1977). Furthermore, each section ends with a summary linking results between taxa and to past findings. Some studies might fall under more than one category of learning and, from each study, only relevant information is presented within a section. With this approach we were able to link results from different species and highlight methodological innovations and shortcomings. We present the full table of relevant studies on non-avian reptiles in Table 1, and below we provide a discussion of this work relevant to each category of learning we defined above.

III. What have we learnt from the last 40 years of studying learning in reptiles?

1. Habituation of behaviour

Habituation is considered one of the simplest forms of learning and occurs when an organism shows a decrease in reactivity after repeated exposure to a stimulus (without motor or sensory adaptation) and allows animals to filter out irrelevant information. Habituation is generally characterised as a short-term change in behaviour. Behaviour at least partially reverts back to its original state after a certain period of time with no stimulation (Rankin et al., 2009; Thorpe, 1963). Initially, habituation was thought to only occur in reflexes but it has since been shown that habituation can occur to responses that are not reflexes including behaviour (Rankin et al., 2009). One of the most famous examples of habituation is the decrease of the gill withdrawal reflex after repeated mechanical

stimulation in the mollusc *Aplysia* (Carew et al., 1972) but habituation likely occurs across all animal taxa (Peeke & Herz, 1973) and has even been demonstrated in plants (Abramson & Chicas-Mosier, 2016). It is not surprising that habituation is widespread, because it is adaptive in many situations. For example, responding to any stimulus with defensive behaviour is a waste of energy and takes time away from other important behaviours such as foraging or reproduction. Across reptiles, the main focus of habituation studies is the habituation of anti-predator behaviour. Below we review the findings and approaches in the sample of identified papers testing habituation from our systematic search for each major group.

Lizards

Iberian wall lizards *(Podarcis hispanicus*) were tested on how personality affects habituation to a simulated predator attack. Boldness, exploration and sociability were recorded for each individual and then groups of eight lizards were released into outdoor enclosures. Across six days, a human observer walked through each enclosure and flight initiation distance was recorded for each individual. Results show that fast but less social lizards habituated faster than slow exploring but social individuals (Rodriguez-Priet et al., 2011).

Snakes

Neonatal common garter snakes (*Thamnophis sirtalis*) habituated their anti-predator response (movement and coiling of the body) towards the movement of a grey card overhead, demonstrating short-term habituation. Half of the animals once again responded after a 15 minute break and all showed anti-predator behaviour towards the card 24 hours later. Furthermore, the number of presentations of the card until habituation decreased across five days which is indicative of long-term habituation (Hampton & Gillingham, 1989). Neonatal Mexican garter snakes (*Thamnophis melanogaster*) but not Butler's garter snakes (*Thamnophis butleri*) habituated to both a moving and non-moving stimulus (the

246 experimenters finger) across five days by decreasing attacks (strikes towards the stimulus)
247 and fleeing across trials. Furthermore, 10 days after the last habituation trial, Mexican garter
248 snakes once again responded to the experimenter's finger (the second species was not
249 tested). In both species, responses were stronger to the moving than non-moving stimulus
250 and both species exhibited individual differences in habituation. In Mexican garter snakes,
251 more reactive snakes habituated faster and litter identity affected habituation. In Butler's
252 garter snake, sex as well as litter affected habituation. Juvenile Mexican garter snakes also
253 habituated to both stimuli showing large individual differences but these were neither
254 dependent on litter identity or sex (Herzog et al., 1989). Adult cottonmouths (*Agkistrodon*
255 *piscivorus*) were also shown to habituate to a simulated predator (snake tongues with a
256 leather glove attached to it) decreasing defensive behaviour (a range of body movements)
257 across five days. Eleven days with no stimulation later, however, their response had not fully
258 recovered (Glaudas, 2004). In a second study, adult snakes significantly decreased
259 defensive striking at the artificial human arm showing habituation while neonate
260 cottonmouths did not habituate (Glaudas et al., 2006). This difference between age classes
261 might reflect a difference in predation pressure in the wild. Young snakes might have more
262 predators and should therefore not habituate as easily as adults. Western diamondback
263 rattlesnakes (*Crotalus atrox*) showed habituation of the rattle response (anti-predator
264 behaviour) in a rattle-box designed to stimulate snakes to rattle by repeated, automatic
265 opening of the lid (Place, 2005). Rattlesnakes decreased rattling as well as latency and
266 duration of rattling within and across four test days, however, individuals showed large
267 variation in all these measures (Place, 2005; Place & Abramson, 2008).
268
269 Summary
270 Overall, adult, juvenile and neonate snakes habituated to a simulated predator attack. In
271 neonates, however, results show a species-specific effect; neonate cottonmouth were an
272 exception and did not habituate to a simulated predator attack. These studies used different
273 methodology and measured different behaviours. It is therefore hard to evaluate if the

difference between species is a species-specific effect or an artefact of methodology. In the past, research has also looked at the habituation of defensive behaviour towards a shadow in turtles and the habituation of attack behaviour towards prey extracts and defensive behaviour in snakes (Burghardt, 1977). To the best of our knowledge, studies investigating habituation of behaviour in lizards are rare with our review only including one such study. Burghardt had already commented on the paucity of habituation studies in reptiles in his 1977 review and our current review shows that this paucity has not been eliminated in the 40 years that followed. It might be argued that habituation has become less interesting when studying learning in reptiles. It is, however, an important learning mechanisms that likely has fitness consequences (although this has not been directly studied in reptiles) and because without habituation to experimental setups and procedures none of the more complex learning studies described below would be possible.

2. Animal training through operant conditioning

Training procedures are increasingly used with reptiles in zoos as enrichment to improve welfare and to be able to perform veterinary procedures without excessive handling of the animals to reduce stress (Hellmuth et al., 2012). However, training procedures might also be used in experimental studies, in which they are often labelled as reinforcement training. The end goal of all these procedures is for an animal to perform a certain behaviour or behavioural sequence which is accomplished through operant/instrumental conditioning which is a form of learning: a desired behaviour is reinforced within a certain context until the animal performs this behaviour reliably within the context. If complex behavioural sequences are the goal, then multiple small steps are usually trained by successive approximation until the more complex endpoint is achieved (Hellmuth et al., 2012). In contrast to habituation, behaviour learned by conditioning is usually long-term and sometimes permanent (Peeke & Herz, 1973). The last 40 years have demonstrated a wide use of training procedures in almost all reptile groups in zoos and for research.

Turtles and tortoises

Turtles and tortoises demonstrated skill in learning different behavioural sequences frequently trained in other vertebrate groups such as target training or the pushing of response keys (Hellmuth et al., 2012). Aldabra tortoises (*Aldabrachelys gigantea*), for example, were successfully trained to associate the sound of a clicker (a commonly used bridge in animal training) with food and later this association was used to train tortoises to walk up to and touch a red target and then extend and lift their heads to make it possible to draw blood. With this target training procedure, animals could learn to move to their night quarters and walk up a ramp to a scale to be weighed improving husbandry while simultaneously removing stress by excessive physical handling (Weiss & Wilson, 2003). Similarly, another group of Aldabra tortoises (*A. gigantea*) was successfully clicker trained and subsequently target trained to a blue-and-white dowel. Furthermore, tortoises were trained to hold the target for 30 seconds. Both behaviours were used to facilitate husbandry and weighing of animals (Gaalema & Benboe, 2008). Galápagos tortoise (*Chelonoidis nigra*) could be trained to extend their neck after touching by a keeper (finch response). For successful holding of the extended neck while touching they received a food reward. The behaviour was subsequently used to facilitate drawing regular blood samples (Bryant et al, 2016).

Certain experimental tests require animals to manipulate objects such as feeders or disks. Painted turtles (*Crysemys picta*), were trained to push response keys to receive a reward. Animals first learnt to eat from an automatic food dispenser and thereafter, had to push an illuminated plastic disk (key) to receive a food reward. The behaviour of pushing response keys was then used to test negative patterning (for details see section III.5) as well as visual discrimination and reversal learning (Blau & Powers, 1989; Cranney & Powers, 1983; Grisham & Powers, 1989; 1990; Powers et al., 2009; Reiner & Powers, 1978; 1980; 1983; Yeh & Powers, 2005). Florida red-bellied cooters (*Pseudemys nelsoni*) and pond sliders (*Trachemys scripta*) both learnt to exit the water, climb a platform and tip bottles for food. First, animals were rewarded for approaching the platform, then for climbing the

platform and finally to tip a plastic bottle. Tipping bottles was then used to test these turtles' discrimination and social learning ability. Impressively, these animals remembered this trained behaviour for 7.5 months without contact with bottles demonstrating that such training can result in behavioural changes that are long lasting (Davis & Burghardt, 2007; 2011, 2012).

Lizards

In a more classical conditioning experiment using a shuttlebox, brown anoles (*Anolis sagrei*) learnt to lift their tail to avoid shock while a second group receiving a shock whenever group one was shocked, did not (Punzo, 1985). Moreover, *Anolis grahami* were conditioned to associate a sound with being pushed off their perch. Two out of three lizards avoided being pushed off by leaving the perch after hearing the sound (Rothblum et al., 1979). Finally, common golden tegus (*Tupinambis teguixin*) learnt to associate a light combined with a buzzer to escape excessive heat into a goal chamber (Yori, 1978).

Similar to turtles, lizards can learn a desired behaviour which was later used to test questions regarding other learning abilities. Eight different studies used successive approximation procedures to teach lizards to remove lids from wells for a reward. First, lizards associated a test apparatus without lids with food. Thereafter, a lid was introduced and a food well gradually covered across trials to teach lizards to remove the lid and get access to a reward. This behaviour was used in experimental settings to test visual discrimination and reversal learning. *Anolis evermanni*, *A*. *pulchellus* and *A. cristatellus* learnt lid removal. The latter, however, were less successful compared to the other two species showing higher levels of neophobia (Leal & Powell, 2012; Powell, 2012). Hatchling three-lined skinks (*Bassiana duperreyi*) also learnt lid removal but only 'hot' incubated lizards acquired this behaviour while hatchlings incubated under 'cold' conditions did not (Clark et al., 2014). Eastern water skinks (*Eulamprus quoyii*) and adult and juvenile tree skinks (*Egernia striolata*) removed lids but neither age class (young and old) or rearing environment (social or solitary) affected performance (Noble et al., 2014; Riley et al., 2018; Whiting et al.,

2018). Moreover, spatial learning proficiency did not predict lid opening ability in water skinks (Qi et al., 2018). Finally, Italian wall lizards (*Podarcis sicula*) and a closely related species *P. bocagei* learnt the same lid-opening technique (Damas-Moreira et al., 2018).

All previous examples were using training procedures to be able to test lizards in different learning experiments. However, lizards are also trained in zoo settings, similar to many turtle species. Hellmuth and colleagues (2012) report that caiman lizards (*Dracaena guianensis*) were successfully trained to associate the sound of a clicker with food. Using this association animals later learnt to touch and follow a target to move into a crait without the need of handling (Hellmuth et al., 2012).

Snakes

Training procedures have also been used to condition different snake species. False water cobras (*Hydrodynastes gigas*), for example, learnt to follow a scented target from their exhibit enclosure to a place backstage where they were fed (data presented by Hellmuth et al., 2012) and sub-adult Burmese pythons (*Python bivittatus*) were first trained to associate a food dispenser with an automatic door with receiving food. Thereafter, these snakes learnt to push a response key next to the door to open it and gain access to the reward (Emer et al., 2015). Finally, Montpellier snakes (*Malpolon monspessulanus*) learnt to move towards a compartment to receive a mouse after the activation of a light (Gavish, 1979).

Crocodiles

A Nile crocodile (*Crocodylus niloticus*) was successfully trained to expect food when hearing a clicker sound. Thereafter, this association was used for target training. The crocodile learnt to approach and touch a black, circular target first in water and later on land. Furthermore, the animal was trained to be touched on the tail to be able to draw blood during veterinary procedures (Augustine & Baumer, 2012).

385 Summary

386 These examples provide solid evidence that conditioning is a great way to teach individuals
387 from all groups of reptiles novel behaviour, from target training to lid removal and the
388 pushing of response keys. These examples also demonstrate how such training is beneficial
389 in both research and husbandry (e.g., zoos, private collections). Examples of classical (or
390 Pavlovian) conditioning, in which a naturally occurring reflex (e.g. limb withdrawal after pain
391 or salivation in the presence of food) is paired with a neutral stimulus (e.g. a bell or a smell),
392 are missing from our review while it was heavily studied in reptiles in the past (Burghardt,
393 1977). This earlier work was important in establishing that reptiles can be conditioned much
394 like other animals. Furthermore, through different techniques research explored dark
395 adaptation, auditory thresholds, olfactory discrimination or colour vision (Burghardt, 1977).
396 Additionally, the application of electric shocks was very common but we found only one
397 study in our search using such negative reinforcement methods (Punzo, 1985). Awareness
398 of reptile welfare is rising (Burghardt, 2013), which likely has led to an increased use of
399 positive reinforcement in animal training and a decrease of Pavlovian conditioning. Positive
400 reinforcement was, nonetheless, already used in the past, although mostly for research
401 purposes to train animals to push levers or response keys (Burghardt, 1977). Burghardt
402 (1977) predicted that the use of operant techniques would become more frequent and our
403 review shows that this is certainly true within zoo settings, if not in laboratory research.
404

405 3. Avoiding aversive stimuli

406 Animals need to know what to eat, when to hide and which threats to avoid. Aversion
407 learning functions to allow organisms to avoid toxic food with a potential noxious effect or
408 avoid dangerous predators. Taste aversion learning, for example, is a conserved ability
409 demonstrated in a wide range of species that is highly adaptive because it aids survival (e.g.
410 Bernstein, 1999). It is, therefore, not surprising to find that reptiles too, quickly learn to avoid
411 food that either tastes bitter or causes illness after ingestion. Mostly, reptilian research into
412 aversion learning has focused on lizards (Figure 2) and a few studies have focused on

413 snakes. Only a single study tested a crocodilian and, to the best of our knowledge, it is still
414 unclear if aversion learning occurs in turtles.
415
416 Lizards
417 Male green anoles (*Anolis carolinensis*), for example, can distinguish between neutral, bitter
418 (coated in quinine hydrochloride) and sweet (coated in Equal®) tasting crickets (a coloured
419 dot improved discriminability). These lizards rejected bitter prey but failed to do so when the
420 vomeronasal organ was blocked, highlighting their reliance on chemical cues (Stanger-Hall
421 et al., 2001). Similarly, hatchling oriental garden lizards (*Calotes versicolor*) associated dish
422 colour with prey taste. Independent cohorts of hatchlings received the same experience:
423 neutral taste in non-painted dishes, sweet taste (from sucrose) in orange dishes and bitter
424 taste (from chloroquine phosphate) in green dishes. When presented with the same
425 combinations they avoided dishes in the colour that had previously contained bitter prey.
426 When lizards were presented with novel colour-taste combinations, however, they attacked
427 bitter prey showing that they had associated dish colour with taste (Shanbhag et al., 2010).
428 Brown basilisks (*Basiliscus vittatus)*, common basilisks (*B. basiliscus*), Schneider's skinks
429 *(Eumeces schneideri)* and common sun skinks (*Eutropis multifasciata*) avoided a novel food
430 one week after a lithium chloride (LiCl) injection (inducing sickness). A second novel control
431 food, however, was accepted one week after a saline injection (Paradis & Cabanac, 2004).
432 Taste aversion has also been demonstrated in the wild. Laurent's whiptail lizards
433 (*Cnemidophorus murinus*) distinguished palatable (soaked in tomato juice) from unpalatable
434 (soaked in quinine hydrochloride) sponges placed in their natural habitat based on visual
435 (green - toxic versus red - sweet) and spatial (ground versus vegetation) cues (Schall,
436 2000).
437 Aversion learning can also be used to train animals to avoid toxic prey. Australian
438 blue-tongue skinks (*Tiliqua scincoides scincoides* and *T. s. intermedia*) fed cane toad
439 sausages (*Rinella marina*, a toxic invader) in combination with a LiCl injection avoided this
440 food for seven weeks. A control group treated with saline showed little to no aversion and

441 both groups accepted sausages of reptile feed fed nine weeks after illness (Price-Rees et
442 al., 2011). In a follow up study, wild-caught blue-tongue skinks (*T. s. intermedia*) were given
443 experience with illness after ingesting a cane toad sausage laced with LiCl. These lizards
444 were then released after recovering and were radio tracked for several weeks. Trained
445 lizards were more likely to survive in the wild after cane toads had invaded their habitat
446 compared to naïve lizards without previous experience. Interestingly, low doses of LiCl that
447 did not induce vomiting in skinks were less effective to condition lizards to avoid cane toads
448 (Price-Rees et al., 2013). Similarly, Ward-Fear and colleagues (2017) trained wild-caught,
449 adult yellow-spotted monitors (*Varanus panoptes*) to avoid cane toads by feeding a test
450 group of lizards with cane toad sausages laced with LiCl, monitored their behaviour towards
451 a live toad (within a mesh container) before and after training (eating chicken necks versus
452 eating cane toad sausages) and compared the changes in interest in the live toad to a
453 control group fed chicken necks only. Test group lizards showed significantly lower interest
454 in the live toad after training with the sausages. All lizards were then released back to the
455 wild and followed to monitor their survival; however, trained lizards were not more likely to
456 survive the toad invasion compared to control lizards. Taking these methods of teaching
457 lizards to avoid toxic toads another step further, in a follow-up study Ward-Fear and
458 colleagues (2016), fed small, juvenile cane toads to wild, free-ranging yellow-spotted
459 monitors (*V. panoptes*) before toads had arrived in the test area to teach them to avoid adult
460 toads. After the arrival of the first toads at the study site, all naïve lizards died within the
461 period of the study while half of the trained lizards survived. In another study, wild, free-
462 ranging yellow-spotted monitors (*V. panoptes*) from cane toad-free populations (Lizard
463 Island, Australia) and from toad-invaded populations (Townsville, Australia) were offered
464 both a dead native frog (rocket frog, *Litoria nasuta*) and a dead cane toad (with the parotoid
465 gland that contain most of the toxin removed) and their behaviour (if they swallowed the food
466 and if they showed any negative reaction after swallowing) recorded. Furthermore, animals
467 from the toad-free population were retested 1-3 days later to see if they had developed an
468 avoidance response towards the novel toxic toads. Naïve lizards, from the toad-free

populations, responded similarly to both dead prey items; however, experienced lizards, from the invaded populations refused to consume the toad (except for one individual) but ate the frog. Retesting revealed that none of the lizards from the toad-free population showed any aversion to consuming dead cane toads; only a few animals, however, showed signs of illness after ingesting toads (Llewelyn et al., 2014). Contrary to these findings in yellow-spotted monitors, lace monitors (*Varanus varius*) from toad-free populations experiencing training with dead toads avoided toads in later trials. Similar to the study in yellow-spotted monitors, free-ranging lace monitors form toad-invaded and toad-free populations were simultaneously presented with a chicken neck, a dead cane toad (without glands) and a dead great barred-frog (*Mixophyes fasciolatus*) and their behaviour recorded. Animals from all populations were retested 1-3 days later to confirm results and toad-naïve lizards were retested 30 days later to record if they had developed toad-avoidance behaviour. Results show that all lizards consumed the chicken neck and the frog but only lizards from toad-naïve populations consumed the toads. 1-3 days later most lizards consumed the frog but none-consumed the toad and finally, 30 days later, animals still refused toads but readily ate frogs. Importantly, three-quarters of lizards that consumed toads showed signs of illness (Jolly et al., 2016). The experience with strong illness after ingestion seems to be most important for avoidance behaviour to develop towards cane toads and for the behaviour to be retained for extended periods of time.

No avoidance to consume toxic fire ants (*Solenopsis invicta*) was shown by wild-caught juvenile eastern fence lizards (*Sceloporus undulatus*) from a population invaded by fire ants, when simultaneously presented with a cricket (*Acheta domesticus*). They increased ant consumption in much the same way as juveniles from a population not invaded by ants (Robbins et al., 2013). In a subsequent study, sub-adult lizards did not avoid toxic ants after direct exposure, after six months (exposed as juveniles), or when they were sourced from a population invaded by fire ants for generations. Similar to the previous study, sub-adult lizards increased ant consumption during the course of the experiment (Herr et al., 2016). A third study used lab-born hatchling fence lizards to test fire ant avoidance behaviour. Naïve

497 hatchlings were presented with (1) eight fire ants (100% treatment); (2) four fire ants and
498 four native ants (*Dorymyrmex bureni*; 50% treatments); or (3) eight native ants (0%
499 treatment) for five consecutive days. Hatchlings from the 100% treatment showed clear
500 aversion learning while individuals in the 50% treatment only avoided ants for one day. Fire
501 ants can be a threat to juvenile lizards because ants might envenomate lizards during
502 consumption, potentially leading to death, although the ants themselves are not poisonous
503 (Venable et al., 2019). Without a strong negative effect, avoidance behaviour might only last
504 a short amount of time (similar to findings in blue-tongue and monitor lizards; see above).
505 Additionally, lizards might learn how to avoid being stung by ants and subsequently
506 incorporate them into their diet later in life.
507 While avoiding harmful food is important, escaping predators is no less crucial for
508 survival. In their natural habitat, red-sided curly-tailed lizards (*Leiocephalus schreibersii*)
509 rapidly learnt to avoid capture. Females did so faster than males and after only one capture
510 event (Marcellini & Jenssen, 1991). Faster predator avoidance could be more beneficial for
511 females especially when, for example, gravid with eggs. In male eastern fence lizards (*S.*
512 *undulatus*) escape behaviour was linked to corticosterone levels. Compared to control
513 animals that increased their flight initiation distance and decreased hiding time, males
514 receiving a corticosterone blocker showed no change in these behaviours and no retention
515 24 h later, demonstrating the importance of steroid hormones in behaviour (Thaker et al.,
516 2010). Moreover, for little brown skinks (*Scincella lateralis*), 48 h of experience with an arena
517 was crucial for escaping a simulated predator attack (moving wall) under a randomly chosen
518 correct refuge. Lizards with no experience of the arena did not learn within the two days of
519 testing (Paulissen, 2008). Furthermore, a second study showed that lizards could use
520 horizontal and vertical stripes to find a ‘safe’ refuge but performed better when presented
521 with vertical compared to horizontal lines, presumably because of the nature of sheltering
522 sites, which are at the base of trees (Paulissen, 2014). Lizards do not just choose a ‘safe’
523 refuge based on patterns, they are similarly skilled using colour and location cues when
524 escaping a threat. Male delicate skinks (*Lampropholis delicata*), for instance, escaped a

simulated predator attack (taping of the base of the tail with a brush) into a 'safe' refuge using location or colour (Chung et al., 2017). More lizards learnt when both colour and location were available compared to colour only. Furthermore, a greater proportion of skinks from natural habitats were successful learners compared to lizards from urban environments (Kang et al., 2018), possibly due to differences in the availability of sheltering sites between these populations. Lastly, behaviour positively correlated with learning performance. Lizards with a fast behavioural type (higher speed and activity, bolder and more sociable) made more errors, showed longer latencies to reach the shelter and took longer to reach the learning criterion. These results indicate a speed-accuracy trade-off in these males (Goulet et al., 2018). Batabyal & Thaker, (2019) quantified habitat composition of rural and urban habitats using satellite images and tested male South Indian rock agamas (*Psammophilus dorsalis*) sourced from these environments on their learning ability and learning flexibility when escaping a simulated predator attack (taping of the tail base). Urban habitats can differ extensively from more natural habitats and vegetation within the targeted urban habitats decreased dramatically within only a few years. Accordingly, lizards from urban habitats learnt better, making fewer errors compared to lizards collected from rural areas. Besides population effects, developmental conditions can also alter escape behaviour. Hatchling White's skinks (*Liopholis whitii*) whose mothers received a low resource treatment (one *Tenebrio molitor* larvae three times per week) were more likely to escape into a 'safe' refuge compared to hatchlings from mothers receiving a high resource treatment (five larvae three times per week) while findings for a colour discrimination task in a foraging context were reversed. One possible explanation for this result proposed by the authors is that the conditions experienced during gestation might prepare offspring for the conditions experienced after birth (Munch et al., 2018a).

Snakes

In plains garter snakes (*Thamnophis radix*) colouration enhances learning of chemosensory stimuli of noxious food. First, snakes were tested for innate aversion to certain visual stimuli.

553 Food was presented in forceps that were either plain, or had coloured (black, green and
554 yellow-black) wings sticking out and attack latencies were recorded. Results showed no
555 innate avoidance of any of the visual stimuli. Next, snakes were separated into three
556 treatment groups: (1) aposematic prey colouration (yellow-black;, (2) non-aposematic
557 colouration (green); and (3) a control group (black) to test how visual and chemosensory
558 cues (different food types) affect learned taste aversion. Fish pieces were offered and then
559 illness was induced in the two test groups by injecting LiCl while control animals were
560 injected with saline. Seven, 12, 17 and 22 days later, snakes were offered two pieces of fish
561 and two earthworms (novel food) with forceps (coloured as per their group) and attack
562 latencies were compared to before training. Both test groups showed aversion learning to
563 fish compared to controls, but the yellow-black group showed the strongest aversion. This
564 effect vanished after 22 days. To confirm this result, the same snakes were retested in two
565 groups: (1) aposematic prey colouration (yellow-black) and (2) non-aposematic prey
566 colouration (green). Animals were again given fish in forceps and illness was induced in both
567 groups. However, seven days later animals were offered each a piece of fish and an
568 earthworm in both yellow-black and green forceps. Again, both groups showed aversion to
569 fish no matter if presented in yellow-black or green forceps but the aposematic group
570 showed stronger aversion (Terrick et al., 1995).
571
572 Crocodiles
573 By using conditioned taste aversion crocodiles can also be taught to avoid novel or invasive,
574 unpalatable prey. Hatchling Australian freshwater crocodiles (*Crocodylus johnstoni*) were
575 given either experience with freshly metamorphosed cane toads (*R. marina*) as prey or no
576 experience. Trained crocodiles were more likely to reject toads compared to naïve
577 individuals (Somaweera et al., 2011).
578

579 Summary

580 These studies highlight how bitter tastes or illness are quickly avoided after only a few
581 encounters which can effectively be used to train vulnerable species to avoid toxic invaders,
582 an important tool for conservation. Studies have used such illness induced aversion learning
583 before, but only in snakes (Burghardt, 1977). Due to its success and value, however, it is not
584 surprising that more and more studies look at aversion learning in reptiles. When individuals
585 are sampled from the wild or trained in the wild, however, care needs to be taken to consider
586 sampling bias. It is well established that only a certain part of a population is sampled with
587 commonly used sampling techniques, often bolder individuals, while shyer individuals are
588 harder to catch (e.g. Biro, 2013; Carter et al., 2012). Personality, amongst other traits,
589 affects learning ability (e.g. Boogert et al., 2018; Dougherty & Guillette, 2018; Sih & Del
590 Giudice, 2012; Volter et al., 2018) and even behavioural morphs within the same population
591 show differences in brain volume (LaDage et al., 2009). Researchers need to acknowledge
592 that sampling bias might have led to biased data not representative of the abilities of the
593 whole population.

594 Escaping predators, too, is a salient stimulus to elicit learning. One important factor
595 that needs to be controlled in studies chasing lizards into hiding is experimenter bias.
596 Unconsciously biasing lizards towards the correct choice during trials might affect results,
597 especially when tests are not conducted blind as to treatment groups (e.g. behavioural
598 types, source population or sex) (Burghardt et al., 2012). For example, researchers may
599 avoid experimenter bias by using a movable wall pushing lizards slowly forward towards a
600 choice apparatus similar to what was used by Paulissen (2008; 2004). Such approaches
601 would also help facilitate experiments being conducted blindly. Interestingly, studies that
602 chase lizards into hiding have only emerged fairly recently. As a new technique little
603 consideration has been given towards evaluating its' effectiveness and how experimenter
604 bias affects results.

605

4. Spatial learning and memory

Navigating the environment is essential when searching or returning for food, shelter or mating partners. Resources and conspecifics are rarely found in the same location. Efficiently navigating as opposed to randomly moving through space may be accomplished by different cognitive processes or navigational strategies. Depending on the information available in the environment, animals employ different strategies such as remembering landmarks, using path integration or even cognitive maps to find their way (Shettleworth, 2010). A variety of studies have investigated the different spatial strategies and cues used by turtles, lizards and snakes to either find food or shelter.

Turtles and tortoises

A red-footed tortoise (*Chelonoidis carbonaria*) adjusted its navigational strategy in a radial-arm maze, a common maze used for testing spatial memory, contingent on the available visual cues in the surrounding environment. In a cue-rich environment, the tortoises used visual cues to find their way around the maze and avoided already visited, food depleted arms (Wilkinson et al., 2007). While in an environment with little visual structure (i.e. when the maze was surrounded by a curtain), the animal fell back on a response-based strategy entering arms next to the last exited arm. Interestingly, when complex visual cues became available again, the animal switched back to using these visual cues to navigate. Which specific features of the environment were used by the tortoise is, however, not clear (Wilkinson et al., 2009). The results obtained in the red-footed tortoise suggest that the spatial strategy applied by animals is dependent on the most useful information available to solve a given task. Accordingly, when pond sliders (*T. scripta*) were presented with a single intra-maze cue acting as a beacon to locate a goal within a plus-shaped maze, turtles reliably used this landmark to find the goal as confirmed by transfer trials, in which individuals started from novel positions. This result was further strengthened when, during probe trials, the beacon was removed making turtles unable to find the goal. A second group of sliders were trained to use an array of extra-maze cues to navigate. Contrary to the cue

trained group, these turtles formed a map-like representation of the maze. Animals were able to find the goal when starting from new locations, when part of the extra-maze cues were concealed but not when all extra-maze cues were removed (Lopez et al., 2000). Unfortunately, no data are available to establish which of the two spatial strategies these turtles prefer when both intra- and extra-maze cues are available. Painted turtles (*C. picta*) were able to learn to navigate an X-shaped maze providing three choice arms. Although extra-maze cues were provided it was not assessed if turtles used these to find the goal (Petrillo et al., 1994). In another study, painted turtles (*C. picta*) transferred a position habit from a T-maze to a X-maze although they started from a different position (Avigan & Powers, 1995).

In rats (*Rattus rattus*) and mice (*Mus musculus*), spatial learning and reference memory are frequently assessed using the Morris water maze, a water-filled pool containing a hidden goal platform (e.g. Vorhees et al., 2006). In a modified version of this task with visible feeders, pond sliders (*T. scripta*) used either a single local cue to guide them to the goal or a map-based strategy based on distal, extra-maze cues (Lopez et al., 2001).

By studying spatial learning in a natural setting using radiotracking, Roth and Krochmal (2015) showed that only resident wild painted turtles (*C. picta*) with knowledge of the habitat used specific routes to find water, while translocated animals without this knowledge failed this task. Importantly, follow-up tests showed that experience, especially during the first few years of life, proved crucial for these turtles to navigate successfully and find a water body. Furthermore, UV but not olfaction was important for spatial orientation (tested in a Y-maze).

Lizards

Unlike the red-footed tortoise, a male jewelled lizard (*Timon lepidus*) navigated the a radial-arm maze using a response-based strategy despite a complex cue environment (Mueller-Paul et al., 2012). Apart from visual cues, reptiles might use the sun to navigate. Male Italian wall lizards (*P. sicula*) located a hidden goal platform in a Morris water maze using a sun

compass. When lizards experienced a clock-shift of 6 h, their search direction shifted accordingly, confirming that these animals used the sun to navigate the maze. Furthermore, by covering the parietal eye, a photoreceptive third eye found on the head, researchers established that it was essential for successful navigation (Foa et al., 2009).

Another commonly used task to asses spatial reference memory in rats is the Barnes maze, a round open space with 10 holes equidistant along the edge. Male side-blotched lizards (*Uta stansburiana*) used extra-maze spatial cues to find the correct hole in a Barnes maze (even after 180° rotation; LaDage et al., 2012). When tested in a round arena including four possible goal rocks similar to a traditional Barnes maze, male Bosk's fringe-fingered lizards (*Acanthodactylus boskianus)* and male Nidua fringe-fingered lizards (*A. scutellatus)* both decreased the time to find a heated goal rock. Detailed analysis of the lizards search behaviour during training and probe trials revealed that *A. scutellatus* used slight markings on the arena wall as local cues to guide their search instead of distal extra-maze cues, while *A. boskianus* did not use either. In a second experiment providing lizards with distant intra-amaze cues, both species again learnt to find the goal indicated by decreasing latencies, however, probe trials were inconclusive as to what strategy animals used. Finally, when a single visual intra-maze cue (a red light) indicated the location of the goal rock, both species learnt but *A. scutellatus* outperformed *A. boskianus.* As an ambush forager, *A. scutellatus* relies more heavily on visual cues compared to *A. boskianus*, an active hunter that uses chemical cues to find prey, which provides a biological basis that may partly explain their differences in information use (Day et al., 1999). In a related study, male little whiptail lizards (*Aspidoscelis inornatus*) navigated the same arena; however, which strategy lizards used to find the goal rock could not be determined. Probe trials suggest that they did not learn through trial-and-error learning or us local, configurational, or spatial cues (Day et al., 2001).

Some studies use semi-natural enclosures to test spatial navigation. Sleepy lizards (*Tiliqua rugosa*), for instance, preferred the location of familiar refuge sites within their enclosure. However, when brightness or shape cues were associated with the refuge,

690 lizards preferred the familiar cue over its spatial location (Zuri & Bull, 2000). Crevice spiny
691 lizards (*Sceloporus poinsettii*) remembered the location of a food patch 24 h later (Punzo,
692 2002) and male eastern water skinks (*E. quoyii*) learnt to escape into a 'safe' refuge avoiding
693 an 'unsafe' hide based on spatial location in a semi-natural outdoor enclosure (Noble et al.,
694 2012); which spatial strategy lizards used, however, was not assessed. In a related study,
695 differences in spatial learning ability could be linked to behavioural type and sex. Bold as
696 well as shy water skinks (measured by the time taken to bask after a simulated predator
697 attack) were more likely to solve the spatial task compared to intermediate type lizards.
698 Furthermore, more males than females learnt within the given amount of trials and males
699 were more likely to choose the 'safe' refuge initially but this difference disappeared by the
700 end of the experiment (Carazo et al., 2014). Although all these studies demonstrate that
701 lizards can learn the location of a refuge, they did not investigate which mechanisms were
702 used to solve these tasks. It is also worth noting that only one study (Carazo et al., 2014), so
703 far, has looked at spatial learning differences between males and females, which are
704 commonly found in other taxa (e.g. great panda: Perdue et al., 2011; hummingbirds:
705 Gonzalez-Gomez et al., 2014; túngara frog: Liu & Burmeister, 2017). These differences are
706 likely common in reptiles, especially lizards, because of sex-specific mating tactics in many
707 species (e.g. Stamps, 1977; 1983), which could be linked to differences in spatial memory
708 proficiency ('range size hypothesis', Jones et al., 2003).

709 In egg laying species, the developing embryos are particularly vulnerable to
710 conditions in the developmental environment. Variable environmental conditions can affect
711 embryonic development resulting in changes in morphology and performance (Noble et al.,
712 2018; While et al., 2018). For example, differences in incubation temperature or oxygen
713 levels can result in differing spatial learning performance. In one species, learning
714 proficiency could even be linked to survival. Hatchling Lesueur's velvet geckos (*Amalosia*
715 *lesueurii*) incubated at 'cold' temperatures were faster spatial learners compared to 'hot'
716 incubated geckos. After release at their mother's capture site, hatchlings with higher learning
717 scores survived longer, indicating a lasting effect on survival (Dayananda & Webb, 2017).

718 Conversely, hatchling three-lined skinks (*B. duperreyi*) incubated under 'hot' conditions
719 earned higher spatial learning scores compared to 'cold' incubated lizards (Amiel & Shine,
720 2012). Moreover, hypoxic conditions (decreased oxygen concentration) during incubation
721 decreased hatchling racerunner lizards' (*Eremias argus*) probability of locating a 'safe'
722 refuge compared to both normoxic and hyperoxic animals. However, error rates were not
723 affected (Sun et al., 2014). While abiotic conditions seem to affect learning, no effect of
724 social rearing environment (social or solitary) was found in juvenile tree skinks (*E. striolata*)
725 solving a vertical maze (Riley et al., 2016). Little is known about how incubation treatments
726 or rearing environment alters the reptilian brain (but see Amiel et al., 2016). The examples
727 above do, however, demonstrate the prolonged influence of environmental effects on
728 behaviour and survival.
729
730 Snakes
731 Three snake species were tested for their spatial reference memory in the Barnes maze but
732 only two species showed successful learning. While juvenile corn snakes (*Pantherophis*
733 *guttatus*) navigated a Barnes maze decreasing distance travelled and errors to below
734 chance on all trials (Holtzman et al., 1999), only half of a group of juvenile spotted pythons
735 (*Antaresia maculosa*) learnt to find the goal. Pythons did not decrease latency and no
736 specific learning strategy could be identified. The Barnes maze was developed for rats and
737 relies on their innate impulse to escape brightly lit, open spaces into a dark escape hole (e.g.
738 Harrison et al., 2006). Conversely, mice do not readily enter these holes and need additional
739 training (e.g. Koopmans et al., 2003). Therefore, some species might be less well suited for
740 testing in this maze. While corn snakes are diurnal and were very active at exploring the
741 arena, spotted pythons are nocturnal and showed little exploration during trials which might
742 explain these different findings (Stone et al., 2000). Rat snakes (*Pantherophis obsoletus*)
743 decreased time to escape a 12 hole Barnes maze but individuals that had been kept in an
744 enriched environment escaped the maze faster than snakes kept under standard conditions.
745 Snakes were provided with intra- as well as extra-maze cues but which ones they used was

not assessed. In some trials prey scent was added to the arena floor which marginally improved performance (Almli & Burghardt, 2006). In a modified version of the traditional Barnes maze using shelters instead of holes in the ground, adult corn snakes (*P. guttatus*) readily used a prominent intra-maze cue fixed to the inner wall when locating the one open shelter amongst four possibilities. During training, all snakes decreased the latency to find the goal shelter and increasingly used a more direct path showing less search behaviour. When the intra-maze cue was moved to a new location within the arena, snakes changed their behaviour accordingly, searching for the goal shelter in the location predicted by the cue (Holtzman, 1998). Similarly, juvenile cottonmouths (*A. piscivorus*) learnt to locate a goal shelter out of four within a round arena. A white card was included as a visual cue. Results showed that snakes learnt the location of the goal during the first day (4 trials), decreasing time to locate the shelter and the distance travelled. Males took 2.5 times longer to locate the goal shelter compared to females and males travelled further (longer distance) than females. Which cues were used, intra- or extra-maze, was again not assessed (Friesen, 2017).

Summary

It is evident that many researchers are interested in how reptiles navigate their environment. Quite a number of studies have utilised open arenas to investigate spatial learning but some have used more ‘traditional’ maze shapes (e.g. X or T) and not all looked at what strategies were used by their test animals to learn the given task, which is important to know if spatial learning occurred. Interestingly, many reptiles, at least to some degree, seem to rely on vison to navigate their environment, which concurs with past research (Burghardt, 1977). Overall, the use of mazes has decreased compared to the past and complex mazes, such as the Lashley maze that includes a number of culs-de-sac, are not used any more (Burghardt, 1977). A few studies have also looked at the involvement of different brain areas or neuroreceptors and transmitter chemicals in spatial learning and navigation in reptiles which have been covered elsewhere (Roth et al., 2019). Overall, we have gained a much

774 better understanding of spatial learning in reptiles. These studies have demonstrated how
775 reptiles use response based strategies, that they can rely on local as well as distal visual
776 cues to find a goal and that if the environment is cue rich they might use map like strategies
777 to navigate. They show how important it can be to have experience with the environment to
778 escape a threat, that different species use different cues to learn (which can sometimes be
779 very subtle) and differences might even arise within species correlating with sex and
780 behavioural types (e.g. bold – shy). Contrary to previous work showing only limited learning
781 ability in snakes (Burgardt, 1977), more recent research shows that these animals can be
782 tested in laboratory settings, hopefully leading to more comparative work in the future.
783
784 5. Learning during foraging
785 While foraging, it is important to discriminate food sources or patches providing food from
786 those already depleted. To save time and energy during searching, animals need to
787 recognise cues associated with food availability (optimal foraging theory; Pyke, 1984).
788 During discrimination learning, animals are presented with a choice of at least two stimuli
789 (such as two colours, patterns or light flicker frequencies), one rewarded and the other not.
790 Many reptiles are proficient in using visual cues including hue, luminance, or shapes and
791 patterns to learn about stimulus-reward relationships.
792
793 Turtles and tortoises
794 Florida red-bellied cooters (*P. nelsoni*), for instance, successfully learnt to discriminate
795 between a bottle including a visual pellet from a bottle without a pellet and retained this task
796 for 12 months (Davis & Burghardt, 2007) and later for 24 months with no interaction with the
797 task (Davis & Burghardt, 2012). Furthermore, red-bellied cooters were able to discriminate
798 between a black and white bottle and retained this ability for 3.5 month with no training
799 (Davis & Burghardt, 2012). Finally, pond sliders (*T. scripta*) also learnt the same black and
800 white discrimination and retained this task for 3.5 months (Davis & Burghardt, 2012). Red-

footed tortoises (*C. carbonaria*) recognise the similarity between real objects and their photographs, although they confused real objects with pictures when presented simultaneously (Wilkinson et al., 2013). Using coloured paddles, common box turtles (*Terrapene carolina*) successfully learnt to select the lighter or darker of two stimuli (out of five shades) and transferred this rule to novel stimuli of different colours (blue and green; Leighty et al., 2013). Painted turtles (*C. picta*) were tested in a negative patterning test, a test for configurational associative learning of compound stimuli in which two single stimuli are reinforced but the compound made out of both stimuli is not. Turtles were first trained on single elements, a red as well as a black and white striped response key. When the compound (white stripes on a red background) was introduced, individuals gradually decreased responding to the compound while continuing to respond to the single elements. In a second experiment testing two-choice discrimination of the single elements, turtles had no problem learning to discriminate between the two stimuli (Powers et al., 2009).

Lizards

Rough-necked monitors (*Varanus rudicollis*) and a Komodo dragon (*V. komodoensis*) used paddle luminance (black and white) to obtain a food reward (Gaalema, 2007; 2011). Male eastern water skinks (*E. quoyii*) relied on colour to solve a three-choice discrimination but no correlation was found between successful learning in the colour discrimination and a previously tested spatial learning task indicating that learning ability is domain specific in these lizards (Qi et al., 2018). In another study, eastern water skinks demonstrated context specific inhibitory skills. Half of the tested lizards learnt to rely on colour the other half on shape stimuli to find a reward. However, some lizards did not learn this discrimination due to a strong side bias. Importantly, learning success in the discrimination task was negatively correlated with success on a detour task. Learners made more errors in the detour task compared to non-learners (Szabo et al., 2019b).

Lizards can also be trained to use light stimuli such as coloured light bulbs to find food. Wild crested anoles (*A. cristatellus*) first received food whenever a yellow or green bulb

was raised and later preferred the trained colour during a simultaneous two-choice test (Shafir & Roughgarden, 1994). Hence, lizards can use multiple visual stimuli to find food while avoiding cues that indicate no food. Not all experiments were, however, successful. Invasive delicate skinks (*L. delicata*) and non-invasive common garden skinks (*Lampropholis guichenoti*) failed to learn the correct arm in a Y-maze setup (one arm painted solid orange or blue, the other in orange or blue stripes) but common garden skinks, overall, showed shorter latencies to reach the goal (Bezzina et al., 2014).

Snakes

Juvenile and adult plains garter snakes (*T. radix*) learnt to discriminate lemon scented pine chips from non-scented chips within 100 trials. Later, adult male snakes were tested in a Y-maze setting in which amyl acetate was diffused into one arm. For some individuals the odour indicated the correct arm, while for others it indicated the incorrect arm. The latter group reached the learning criterion in fewer trials (Begun et al., 1988). Juvenile cottonmouths (*A. piscivorus*) could learn to rely on a red card to find food. Animals were tested in two groups, in the test group the red card predicted in which food bowl a live fish could be found, while in the control group the card was randomly allocated and therefore did not predict in which bowl the fish could be found. After 14 days of training, test group animals showed foraging postures in front of the bowl indicated by the red card only, while control group animals performed at chance level. After 25 days with no training, test group animals performed similar to control group snakes showing no long lasting memory of this discrimination (Friesen, 2017).

Tuatara

A single study tested discrimination learning using a simultaneous two-choice test in 17 juvenile tuataras (*Sphenodon punctatus*). Animals were able to discriminate between a constant light and light flickering at frequencies of 14.08, 25.06 and 45.61 Hz but failed when

a constant light and a light flickered at a frequency of 65.09 Hz were presented simultaneously (Woo et al., 2009).

Summary

Reptiles are able to discriminate between a wide range of visual stimuli in two-choice setups and studies in turtles show that they can remember such learnt discriminations for long periods of time. Such memory studies are, however, rare in other reptile groups. In some studies, rather complex learning rules were used such as in tasks of negative patterning (Powers et al., 2009), knowledge transfer between real objects and pictures (Wilkinson et al., 2013) or discrimination based on lighter/darker colour (Leighty et al., 2013). Patterns, shapes, coloured papers and coloured light were frequently used in the past; however, the focus of previous visual two-choice discrimination tasks was mainly the investigation of colour vision and visual acuity as well as visual thresholds. Knowledge transfer, generalisation and rule learning have previously been demonstrated in different reptiles species (Burghardt, 1977). In his review, Burghardt (1977) reported a lack of evidence for learning in most studies, which has certainly changed. Interestingly, many species described in Burghardt's (1977) review took hundreds of trials to reach criterion, with the biggest issue being the development of position habits (a side bias). It is still not clear why animals develop such side biases in some cases while not in others. Choice of stimulus might factor into this issue. If animals are unable to properly perceive a stimulus or are unlikely to consider it a cue then falling back onto a one-sided response might be an alternative strategy to maximise gain. It is therefore very important to consider which stimuli are used in learning tasks. An inability to solve a given task might just be caused by non-cognitive factors rather than an issue with processing. Together, the focus of research has shifted towards how reptiles learn rather than that they can discriminate between stimuli. Furthermore, discrimination learning in snakes was largely ignored in the past (Burghardt, 1977) and even now, such research is rarely conducted.

6. Quality and quantity discrimination

Judging non-symbolic quality and quantity are important capabilities during foraging, mate choice or when making decisions about joining a group (e.g. shoal choice in fish; e.g. Buckingham et al., 2007). Quantity discrimination has been demonstrated in a wide range of animals from insects (e.g. Pahl et al, 2013) to fishes (e.g. Agrillo & Bisazza, 2018), mammals (e.g. Abramson et al., 2011; Benson-Amram et al., 2018; Hanus & Call, 2007; Uller & Lewis, 2009), birds (e.g. Bogale et al., 2014; Garland et al., 2012; Rugani et al., 2018), and amphibians (e.g. Stancher et al, 2015; Uller et al., 2003). With the addition of data on three turtles and one lizard species, basic numerical abilities (judging differences in quantity) have now been confirmed for all vertebrates.

Turtles and tortoises

After associating a stimulus with a specific reward quality or quantity, red-footed tortoises (*C. carbonarius*) selected the larger quantity during the simultaneous presentation of two stimuli differing in value. Furthermore, tortoises remembered these relative quantities/qualities for 18 months (Soldati et al., 2017). Turtles are generally long-lived and are good models for studying long-term memory. The speed with which Reeves' turtles (*Mauremys reevesii*) moved down a runway was also contingent on the magnitude of food reward provided at the end. Turtles receiving 24 pellets each trial moved faster than turtles receiving only two pellets. During extinction trials, with no food present, animals previously receiving large quantities took longer to extinguish responding than animals previously trained with less reward (Papini & Ishida, 1994). In a spontaneous discrimination test, Hermann's tortoises (*Testudo hermanni*) successfully chose the larger size and quantity of tomato (Gazzola et al., 2018) in four different combinations: 1 versus 4, 2 versus 4, 2 versus 3 and 3 versus 4 (ratios 0.25, 0.5, 0.67 and 0.75, respectively). Performance followed a ratio effect; the smaller the ratio the better accuracy in choosing the larger quantity/size of food.

911 Lizards

912 Similar to the Hermann's tortoises, Italian wall lizards (*P. sicula*) spontaneously
913 discriminated between two food items (dead fly larvae) differing in size (ratios 0.25 to 0.75).
914 They did, however, not select the larger of two quantities but performance in the size
915 discrimination test again followed a ratio effect (Petrazzini et al., 2017). When the same
916 species was later tested on a trained discrimination of both size and quantity, lizards
917 discriminated between 1 versus 4 (N = 6/ 10) and 2 versus 4 (N = 1/ 6), but not between 2
918 versus 3 yellow disks and none were able to discriminate between two differently sized disks
919 (ratio of 0.25; Petrazzini et al., 2018). These conflicting results might be explained by
920 differences in the stimuli used. Motivation to approach artificial stimuli might differ from
921 motivation towards actual food items.

922

923 Summary

924 Quantity discrimination abilities are undoubtedly important for survival. It is therefore not
925 surprising that reptiles also possess at least rudimentary abilities to discriminate based on
926 food quantity and quality. From these few studies, it has become clear that there are
927 differences between species and the reasons for these differences are in need of further
928 investigation. As far as we are aware, tests of quantity discrimination have not been done in
929 the past which highlights our very limited knowledge compared to other vertebrate groups
930 (Agrillo, 2015). We believe that future studies looking into reptile numerical abilities will
931 greatly advance our understanding of this cognitive ability. Both the study of spontaneous
932 and trained quantity discrimination will certainly be of great value to the field (Agrillo &
933 Bisazza, 2014). Using artificial stimuli (used during trained quantity discrimination) as
934 compared to natural stimuli such as food items (used during spontaneous quantity
935 discrimination) might be less successful in reptiles. However, reptiles can recognise food
936 items from photographs (Wilkinson et al., 2013), which could be used as an alternative.

937

7. Responding to change

Flexibly responding to environmental stimuli and adapting to change quickly is important for survival especially in unpredictable environments (Lefebvre et al., 2004). Behavioural flexibility, the ability to adjust to environmental variation by adapting attention and behaviour and using existing skills to solve novel problems or existing problems in a new way, can be measured through different tests. One index of behavioural flexibility is a test of reversal learning ability, when a previously established stimulus-reward relationship changes (Brown & Tait, 2015). Rather rare are tests of attentional set-shifting, another index of behavioural flexibility (Brown & Tait, 2015; Roberts et al., 1988). Attentional set-shifting tasks usually incorporate multiple two-choice discrimination stages (including reversals) of multi-dimensional stimuli. Animals first learn to rely on one dimension to receive a reward and to disregard the other dimensions (development of an attentional set). In the crucial stage, the stimulus-reward relationship is moved to a previously unimportant dimension and animals need to shift their attention towards this dimension (Brown & Tait, 2015). Finally, innovative problem solving tasks (Auersperg et al., 2014) have, so far, not been used to investigate behavioural flexibility in reptiles.

Turtles and tortoises

Reeves' turtles (*M. reevesii*), for instance, reversed a simple left/ right discrimination. Turtles that were over-trained on the initial discrimination for an additional 100 trials, however, reversed more slowly (Ishida & Papini, 1997). Moreover, red-footed tortoises (*C. carbonaria*) transferred knowledge about a food patch (left/ right food bowl) acquired on the touchscreen to a real-life setup but did not transfer knowledge about a reversal trained on a real life set-up back to the touchscreen (Mueller-Paul et al., 2014). When tested on a visual (colour plus shape) discrimination in a y-maze, red-footed tortoises developed a side bias during reversals although a pilot study indicated no strong tendency to choose one side over another. Despite this bias, tortoises were able to successfully learn during four successive reversals and trials to criterion decreased to training performance (initial acquisition) by the

second reversal (Bridgeman & Tattersall, 2019). Finally, painted turtles (*C. picta*) performed multiple reversals and extra-dimensional shifts of colour and pattern (stripes) stimuli. Colour reversals were the most difficult for the animals, even more difficult than dimensional shifts (Cranney & Powers, 1983).

Lizards

Male rough-necked monitors (*V. rudicollis*), one Komodo dragon (*V. komodoensis*; Gaalema, 2007; 2011) and five western banded geckos (*Coleonyx variegatus*; Kirkish et al., 1979) increased performance during serial reversals. In rock agamas (*P. dorsalis*), habitat features (vegetation cover) affect reversal learning proficiency. Lizards learnt to escape into a 'safe' refuge during a spatial reversal conducted in a controlled lab setting but animals collected from urban areas made fewer errors compared to lizards from rural areas (Batabyal & Thaker, 2019). Wild eastern water skinks (*E. quoyii*) likewise learnt to locate a 'safe' refuge to escape a simulated attack even after a spatial reversal in semi-natural conditions (Noble et al., 2012), and little whiptail lizards (*A. inornatus*) avoided a heat lamp using features (colour, brightness or pattern) or the location of a 'safe' refuge in a reversal. During acquisition spatial cues were more salient to these lizards than visual cues but not during reversals (Day et al., 2003).

A test of multiple species with the same methodology in three anoles (*A. evermanni*, A. *cristatellus* and A. *pulchellus*) revealed less behavioural flexibility in a reversal task in *A. cristatellus* compared to A. *evermanni* and A. *pulchellus*. Differences were attributed to neophobia but sample sizes were small (Leal & Powell, 2012; Powell, 2012). Similarly, *A. boskianus*, an active forager, learnt faster during reversals applying the fork method (one spine holding the reward while the second spine provided a visual cue) compared to *A. scutellatus*, a sit-and-wait forager. Active foraging might require better inhibitory skill, crucial in reversal learning, to inspect prey before striking (Day et al., 1999).

Tree skinks (*E. striolata*) were the first lizard species to be tested using an attentional intra-dimensional/ extra-dimensional (ID/ ED) set-shifting approach. Unexpectedly, lizards

994 did not establish an attentional-set but performed each set of two stages (discrimination and
995 reversal of one stimulus pair) as if facing a new problem. Skinks, however, reversed four
996 discriminations showing some degree of flexibility in response behaviour (Szabo et al.,
997 2018). In a subsequent study using the same methodology in blue-tongue lizards (*T. s.*
998 *scincoides*), no evidence of set-formation was detected either. The study revealed, however,
999 that juveniles learnt at adult levels throughout all set-shifting stages effectively
1000 demonstrating adult-level cognitive ability in young precocial lizards. This result implicates
1001 that juvenile precocial skinks might be born with enhanced cognitive ability that could give
1002 them an advantage during early life in the absence of parental care (Szabo et al., 2019a);
1003 however, data on a less precocial lizard species exhibiting rudimentary forms of parental
1004 protection (e.g. some of the family living lizard species; but see Whiting & While, 2017) is
1005 needed to confirm this hypothesis.
1006 In European glass lizards (*Pseudopus apodus*), both lizards with damage to the
1007 hippocampus and lizards with lesions to the DVR (dorsal ventricular ridge) took longer to
1008 learn a reversal (distinguishing between a triangle and a circle) compared to normal lizards.
1009 Results show that hippocampal lesions affect inhibition while lesions to the DVR affect visual
1010 processing (Ivazov, 1983).
1011 As ectotherms, reptiles rely on environmental temperature to reach optimal
1012 physiological function. Temperature also plays an important role during embryonic
1013 development. Many reptile species exhibit temperature dependent sex determination (Bull,
1014 1980). Even in species with chromosomal sex determination, deviations from normal
1015 incubation temperatures can alter brain morphology and consequently, learning ability. For
1016 example, in hatchling three-lined skinks (*B. duperreyi*), incubation treatment (‘hot’ versus
1017 ‘cold’) affected discrimination of lid colour. Only ‘hot’ incubated lizards learnt the given tasks
1018 including a choice reversal (Clark et al., 2014). These differences in performance were
1019 linked to differences in cortex size and structure. ‘Hot’ incubated lizards had a smaller
1020 telencephalon but increased neuron density in certain cortical areas (Amiel et al., 2016).
1021

1022 Snakes

1023 Juvenile and adults plains garter snakes (*T. radix*) reversed an initially learnt discrimination
1024 between lemon and unscented pine chips within 50 trials. Before the reversal, snakes, on
1025 average (five-trial blocks), chose the lemon scented compartment at a level of about 80%
1026 correct while directly after the reversal, choices dropped down to chance level. Gradually,
1027 snakes chose the compartment with the unscented pine chips until about 70% correct at the
1028 end of 50 trials (Begun et al., 1988).

1029

1030 Summary

1031 In recent years, reversal learning has increasingly been used as a test of behavioural
1032 flexibility in reptiles, although by itself it is likely insufficient. This is in part because most
1033 species tested to date are capable of reversal learning. Combining reversals with related
1034 tests of innovative problem solving (e.g. Auersperg et al., 2014; Leal & Powell, 2012) or
1035 attentional set-shifting (Szabo et al., 2018; 2019a) could be a more robust approach to
1036 investigate behavioural flexibility. Subjects use of, for example, different techniques to solve
1037 a novel problem or quick shifting to a previously untrained attentional set (to a stimulus in a
1038 e.g. second, formerly irrelevant dimension; Brown & Tait, 2015) could provide stronger
1039 evidence for behavioural flexibility. In the past, studies looked mostly at serial reversal
1040 learning but not as a means to investigate flexibility in behaviour but rather as a measure of
1041 intelligence (Burghardt, 1977). Serial reversal tasks have become less frequent and single
1042 reversal studies have increased. Furthermore, no data on reversal learning in snakes was
1043 available previously (Burghardt, 1977), showing a trend towards testing of a phylogenetically
1044 wider range of species. Researchers are also starting to use the methods of comparative
1045 psychology by testing reptiles in tasks such as attentional set-shifting (Szabo et al., 2018,
1046 2019a). Such interdisciplinary work will likely become more frequent and will help us better
1047 understand behavioural flexibility in reptiles while also making comparisons with other
1048 vertebrates.

1049

8. Solving novel problems

Some species are known to be good at solving complex problems. For example, New Caledonian crows (*Corvus moneduloides*) that bend wire into hooks in order to extract a reward-containing basket from within a well (Weir et al., 2002), or black rats (*R. rattus*) that develop new techniques for extracting pine seeds from cones when little other food is available (Zohar & Terkel, 1991) are just two examples of innovation and problem-solving skills. Reptiles can also learn novel foraging techniques.

Turtles and tortoises

Painted turtles (*C. picta*), for example, learnt to push response keys (Blau & Powers, 1989; Cranney & Powers, 1983; Grisham & Powers, 1989; 1990; Powers et al., 2009; Reiner & Powers, 1978; 1980; 1983; Yeh & Powers, 2005) and Florida red-bellied cooters (*P. nelsoni*) and pond sliders (*T. scripta*) both exited water to climb a platform and tip bottles for food, which can also be interpreted as a novel foraging technique (Davis & Burghardt, 2007; 2011, 2012).

Lizards

Eight different studies have used training procedures to teach lizards to remove lids from wells for a reward and although training preceded the tasks, these are examples of reptile species solving novel problems (Clark et al., 2014; Damas-Moreira et al., 2018; Leal, & Powell, 2012; Noble et al., 2014; Powell, 2012; Qi et al., 2018; Riley et al., 2018; Whiting et al., 2018). Only two studies attempted to test a reptile on a puzzle box task. Black-throated monitors (*Varanus albigularis albigulari*s) opened a plastic tube to retrieve a reward within 10 minutes of the first presentation and solved this novel task faster during the second and third trial (Manrod et al., 2008). Using a modified version of this tube task, Cooper and colleagues (2019) tested one roughneck monitor (*V. rudicollis*), two emerald tree monitors (*V. prasinus*), two Mertens' water monitors (*V. mertensi*), two Guatemalan beaded lizards (*Heloderma*

charlesbogerti) and one Jamaican iguana (*Cyclura collei*). Of the five species, the iguana could not be tested because of low motivation (it did not approach the tube) and only individuals of two (*V. prasinus and V. mertensi*) out of the remaining four species showed evidence of learning (decrease in the time needed to open the tube). Over 40 trials were given and individuals needed up to 30 minutes to retrieve the reward. Both the snout and claws were used by animals to open the tube but to a differing degree depending on the species' foraging behaviour (i.e. digging or hunting with claws versus digging or hunting with the snout) (Cooper et al., 2019).

Snakes

Similar to turtles, wild Burmese pythons (*Python bivittatus*) successfully learnt to push a response key to open a door to gain access to a reward (Emer et al., 2015). This trained behaviour was, however, not used in further tests.

Summary

Reptiles can be trained to perform complex behaviours and some species are proficient in opening puzzle boxes. However, little research has examined complex problem solving in reptiles. Puzzle boxes used in the past were quite simple – tubes with hinged doors – but how reptiles would perform when given more complex tasks that might need several steps to solve is unclear as of yet. Arguably, it is quite hard to design such problem-solving tasks for reptiles because they do not use their front legs or mouths like mammals and birds do. With some cleverly designed tasks, however, we firmly believe that reptiles will show good problem-solving skills and we want to encourage researchers to demand more from their reptilian subjects by applying more complex problem-solving tasks.

9. Social learning

Social learning refers to learning from other individuals (conspecifics or heterospecifics)

used as a shortcut to solve novel problems and in the process, avoid costly trial-and-error learning. Social learning comprises several abilities from simple enhancement and facilitation to imitation and emulation (Byrne, 1994; Heyes, 1994) and can be beneficial for social species as well as more solitary animals (Galef & Laland, 2005; Shettleworth, 2010). Nonetheless, research has focused mainly on group living animals' social learning ability, much less is known about social information use in less social species (Galef & Laland, 2005). Recent work has shown that even less social reptiles can learn from their conspecifics. So far, social learning has only been studied in six lizard and two turtle species and it is likely to be more common in reptiles than previously believed.

Turtles and tortoises

Florida red-bellied cooters (*P. nelsoni*) were the first reptile species to show social learning. Turtles matched the choice of a demonstrator during a brightness discrimination, demonstrating stimulus enhancement (Davis & Burghardt, 2011). Later, solitary living red-footed tortoises (*C. carbonarius*) demonstrated social learning in a detour task (Wilkinson et al., 2010). Tortoises that observed a demonstrator walking around a barrier learnt to detour for a reward, while a control group with no demonstration did not. During follow-up experiments, observers were able to generalise to novel barriers (inverted V- and U-shaped) and were more successful than control turtles (Wilkinson & Huber, 2012).

Lizards

Solitary bearded dragons (*Pogona vitticeps)* opened a sliding door in the same direction as a demonstrator after watching a video of a conspecific's performance. A control group watching a ghost control (door opening by itself) did not learn to open the door, indicating some involvement of socially facilitated enhancement (Kis et al., 2015). Interestingly, 'cold' incubated hatchling bearded dragons were faster at opening a door after demonstration than 'hot' incubated lizards. There was, however, no significant difference between groups in the

number of successful door openings (Siviter et al., 2017). Wild Lilford's wall lizards (*Podarcis lilfordi*) preferred locations with conspecifics present when given a choice between food with and without conspecifics (including static copper models). Lizards also preferred to aggregate with conspecifics (trapped in a glass jar) instead of an empty glass jar when no food was present. These lizards occur in high densities, are generalist foragers and conspecifics can be a reliable source of information regarding foraging opportunities (Perez-Cembranos & Perez-Mellado, 2015).

Age or sex can affect the probability with which animals employ social information (Galef & Laland, 2005). In eastern water skinks (*E. quoyii*), age but not dominance status predicted if lizards learnt a two-choice discrimination from a conspecific. Lizards selected the correctly coloured lid out of two coloured lids with and without a demonstration; young males, however, learnt faster than controls while older lizards did not (Noble et al., 2014). In a follow-up study on the same species, Kar et al. (2017) disentangled age and dominance by manipulating dominance status of water skinks and presenting them with similar learning tasks. Dominant observers learnt faster than subordinate observers during task acquisition but not during reversals suggesting social learning is indeed age-related and not the result of age-dominance correlations (Kar et al., 2017). Water skinks are often found in high densities around water bodies (Cogger, 2014) and social information is therefore readily available.

Social learning improves acquisition of crucial information that is essential for naïve individuals (e.g., juveniles) or when facing novel challenges (Galef & Laland, 2005). Although reptiles are considered mostly solitary, Australia is home to an exceptional group of skinks, the *Egernia* group (nine genera), with species varying in their degree of social complexity from solitary species to monogamous species living in multi-generational family groups (Chapple, 2003; Gardner et al., 2008; While et al., 2015). One such species is the monogamous White's skinks (*L. whitii*), in which familiarity can improve social information use during reversal learning but not during acquisition. In a study by Munch and colleagues (2018b), White's skinks were tested in three treatment groups: Individuals observing their mating partner (demonstrator), an unfamiliar conspecific (demonstrator), or a non-

demonstrator (control). Lizards observing their mate reversed faster than controls (Munch et al., 2018b). Reversals are expected to be more challenging. As such, social information may be more valuable for reversal tasks. Conversely, juvenile tree skinks (*E. striolata*), also a family living Egernia group species, did not use information provided by an adult in a similar discrimination task. Furthermore, rearing treatment (social or solitary) did not affect discrimination or reversal learning (Riley et al., 2018). Although tree skink families stay together for at least one season (Whiting & While, 2017) and juveniles have the opportunity to learn from parents, learning from just any adult might be costly because juveniles experience a high risk of cannibalism from unrelated adult conspecifics (O'Connor & Shine, 2004; While et al., 2015) and therefore, they may be less likely to use them as a source of social information. Adult females of the same species do readily learn a two-choice discrimination from other, familiar females showing a decrease in errors and faster learning compared to a control group (Whiting et al., 2018). Using a familiar parent as a demonstrator for juveniles might lead to different results.

Typically, animals are tested with conspecific demonstrators but it can also be beneficial to learn from heterospecifics which has been tested in one reptile species, the Italian wall lizard (*P. sicula*). This species has been introduced to a number of regions outside its natural distribution across the globe (CABI, 2018) including locations with other congeneric species of the genus *Podarcis*. This situation creates a novel opportunity to test if *P. sicula* exploit social information from congeneric lizards that are not dissimilar to themselves. Accordingly, when tested on a colour discrimination task in which information was provided either from a conspecific or a heterospecific (*P. bocagei*) species, observer lizards made fewer errors regardless of demonstrator species compared to individual learners (Damas-Moreira et al., 2018). These results suggest that social information use might play some role during establishment in a novel habitat.

Summary

Reptiles are generally viewed as solitary, ‘asocial’ animals. However, despite the fact that

most reptiles species do not group in the same way mammals or birds do, many species form territories and have territorial neighbours (e.g. Brattstrom, 1974; Pianka & Vitt, 2003). In some species, individuals come together during the mating season (e.g. Brattstrom, 1974; Pianka & Vitt, 2003), group in overwintering sites (e.g. Brown & Parker, 1976) or at basking spots (e.g. Amarello, 2012 cited by Waters et al., 2017; Brattstrom, 1974; Pianka & Vitt, 2003) and sometimes juveniles tend to group together (e.g. Burghardt, 1983). Some adults even protect their young for at least some period of time (e.g. Butler et al., 1995; Garrick et al., 1978; Schuett et al., 2016; Whiting & While, 2017). Importantly, some reptile species form long-term family groups (e.g. Whiting & While, 2017). All these instances provide opportunities for social information transmission; Suboski (1992) previously regarded the behaviour shown by some reptiles as simple forms of social learning (enhancement and social facilitation). Research since the early 2000s has demonstrated that reptiles learn socially. Now it is time to delve into more detailed studies on what is learned, from whom, and when (Laland, 2004).

IV. Future directions

In the last 40 years, since the first detailed review by Burghardt (1977) on reptile learning, we have seen a steady increase in reptile cognition research after a sudden drop (Figure 1). In the last 10 years, there has been an even greater resurgence in cognition research using these amazing animals with this acceleration being first highlighted by Wilkinson and Huber (2012) and Burghardt (2013). In some respects, we have gained a better understanding of reptile learning abilities more generally as new species have been tested and new methodologies have been developed. Interestingly, research with turtles has decreased while lizards have become much more popular research subjects (Figure 1, 2 and 3). Overall, the focus of the field has somewhat changed. Studies investigating habituation of behaviour are still rare and operant conditioning as part of animal training has become popular in zoos to improve reptile welfare but has become less common in basic research.

Aversion learning is now an increasingly used tool in conservation to train animals to avoid novel toxic invader species. Spatial learning is still well studied but comparative approaches investigating why species or individuals differ in their abilities are rare. Overall, research now focuses more on learning performance but how, for example, a discrimination is learnt is still poorly understood. Behavioural flexibility tested using reversal learning tasks is widely studied in turtles and lizards but less so in snakes. Other tests of behaviour flexibility including problem-solving tasks should improve our understanding of how flexible reptiles really are when environmental conditions change. Social learning and quantity discrimination in reptiles are new research areas that have only emerged very recently while partial reinforcement studies, probability learning and classical conditioning are not studied any more. Some cognitive processes such as executive function have yet to receive proper attention in reptiles. Here, we present some key themes and questions that we believe are particularly interesting topics for future research that have emerged as key components missing from our literature review.

1. The fitness consequences of individual differences in cognition

The potential relationship between cognitive processes and fitness has received increasing attention this past decade (e.g. Huebner et al., 2018; Madden et al., 2018; Thornton et al., 2014) because to understand the evolution of a cognitive trait we need insight into how selection acts on it. Research into reptile personality, defined as individual differences in behaviour that are consistent across time and context, has demonstrated low levels of heritable variation for many behavioural traits. Nonetheless, it has been demonstrated that female behavioural type affects offspring survival (for more details see Waters et al., 2017). Cognitive ability (domain general or specific), similar to personality, might also change an individual's fitness in a myriad of ways (e.g. foraging ability, learning resource distribution; location of safe refuges, etc.). Although this is widely assumed, it is less often supported by empirical data (e.g. Healy, 2012; Thornton et al., 2014). Forty years ago, Burghardt (1977) had raised the question: "What are the selective pressures and cost-benefit relationships

involved [in learning] ?" In our review, only one study tested how success in a learning task predicted survival; geckoes that were better learners survived longer, potentially leading to greater future reproductive success (Dayananda & Webb, 2017). While the precise mechanism(s) by which spatial learning improves survival in geckos is still not understood, we want to encourage more research into the links between cognition and fitness. For example, does cognitive ability influence survival directly and/or, does it affect reproductive success and does cognitive ability correlate with some other trait? In relation to reptiles, learning the location of safe refuges in their environment, the location of thermally suitable refugia, the spatial variation of prey/food and information about social structure/dominance of individuals in their social neighbourhoods, could all potentially influence fitness. With more research into individual differences in cognitive ability and better insights into how these differences might relate to fitness (assuming cognitive ability is heritable in reptiles similar to what was found in other taxa: e.g. Galsworthy et al. 2005; Hopkins et al. 2014) we will be able to better understand the evolution of cognitive traits.

2. Cognition in ecologically relevant contexts

The ability to learn is shared by all animals, the proficiency with which a species learns about certain stimuli depends, however, on the degree to which selection has operated on a given cognitive process in the wild (Shettleworth, 2010). Few studies covered in our review attempted to test learning in the wild (e.g. Marcellini & Jenssen, 1991; Roth & Krochmal, 2015; Schall, 2000; Shafir & Roughgarden, 1994), or even in ecologically relevant contexts in the lab or captivity (e.g. Foa et al., 2009; Price-Rees et al., 2011; Robbins et al., 2013; Somaweera et al., 2011). Inadequate attention to a species' ecology can dramatically affect study results and affect generality of inferences (Holtzman et al., 1999; Stone et al., 2000), an issue that has been raised before (Burghardt, 1977) but has still received too little attention.

By taking species ecology and life history into account, we will enhance the validity of the results generated by cognitive studies. Testing cognition in the wild will make results

more biologically relevant, although we appreciate how challenging this can be with reptiles (see also Whiting & Noble, 2018). For questions that are only testable within a controlled laboratory setting (as compared to studies in the wild), using wild-caught individuals (accounting for prolonged negative effects of captivity, e.g. Mohammed et al., 2002) could be a suitable alternative although individuals need to be properly acclimated to the laboratory conditions because the stress of captivity and testing might alter behaviour and affect results (Bailey, 2018; Langkilde & Shine, 2006). Nonetheless, using wild caught individuals could also circumvent any issues associated with decreased cognitive ability from being raised in captivity (du Toit et al., 2012). Adequate reporting on the origin of animals is high in studies testing squamates (lizards and snakes) while in turtles more than half did not report the origin of test animals (Table 1). Furthermore, information on the duration animals were maintained in captivity is scarce. We encourage researchers to improve on reporting of critical study details and to select study species while considering whether their ecology and life history are appropriate for their research question. For example, nocturnal species should be tested in the dark under red light, and as ectotherms, reptiles depend on the temperature of the environment to heat their body to reach optimal physiological function which can have a major impact on response time and motivation (Burghardt, 1977; Whiting & Noble, 2018). For active foragers, that rely on prey odour during foraging, task design needs to control for olfactory cues while it is less important for sit-and-wait foragers because they rely more heavily on vison (Cooper, 1995). These are just a few parameters that need to be considered when designing laboratory studies in reptiles (for more details see Whiting & Noble 2018).

3. Cognition and behaviour in invasive species

Introduced species outside their natural range can have detrimental effects on local communities (e.g. Reaser et al., 2007). For example, the brown tree snake (*Boiga irregularis*), native to parts of Australasia, was introduced to Guam causing a major decrease in, and extinction of, native bird populations within a few decades (Lowe et al.,

2000). Similarly, the red-eared slider (*T. scripta elegans*), has spread from its natural range in North America to all over the world including Europe and Australia, threatening native turtle species by competing for resources (Burger, 2019). The mechanisms favouring the successful invasion of a species into a new habitat are of major interest but, unfortunately, traits benefiting the establishment of new populations are species and habitat specific. No general factor increasing invasion success across species has emerged (Hayes & Barry, 2008; Kolar & Lodge, 2001). Success and failure during invasion have been linked to behaviour and personality (Amiel et al., 2011; Chapple et al., 2012) but how learning benefits individuals has received little attention (Avargues-Weber et al., 2013). Social learning and behavioural flexibility might play an important role during the early stages of establishment when animals frequently face novel predators or prey. Using information from congeneric species or flexibly changing behaviour could be key to survival (Sol et al., 2002; Wright et al., 2010). It has been demonstrated that invasive lizards are able to effectively use information provided by heterospecifics (Damas-Moreira et al., 2018) and that they are more plastic compared to sympatric, non-invasive congeneric species (Damas-Moreira et al., 2019). Furthermore, past experience with competition (e.g. Yeager & Burghardt, 1991), prey (e.g. Arnold, 1978; Burghardt & Krause, 1999; Clark, 2004; Mori, 1996; Shafir & Roughgarden, 1998; Stimac et al., 1982) and predation (e.g. Desfilis et al., 2003; Herzog, 1990) can have a lasting effect on how individuals react in future situations. These studies, however, are only a first step in understanding which cognitive abilities might benefit invasive species more when conquering novel challenges. Future research could focus on comparing performance in different tasks (foraging, social and spatial learning) between species known to be successful and unsuccessful invaders.

4. Social learning in social reptiles

Social learning is usually studied in group living animals (Galef & Laland, 2005) because it is hypothesised that the demands of group living act as a selective pressure to improve cognition (and increase brain size) to cope with these demands (Humphrey, 1976; Jolly,

1966; Reader & Laland, 2002). Less social reptiles, however, are also capable of social learning (e.g. Noble et al., 2014; Wilkinson et al., 2010). We agree that testing non-social species is an important research endeavour, but we want to encourage researchers to also test social reptiles (Whiting & While, 2018). Although reptiles have demonstrated the ability to learn from conspecifics in controlled lab-setups, it is less clear if such social information use also occurs in the wild. It would be interesting to see how wild reptiles react to a conspecific trying, for example, some unusual prey or using a novel technique to gain access to a previously inaccessible food source. By using video recordings (e.g. Siviter et al., 2017; Kis et al., 2015) researchers can exert control over task parameters and gain insight into which information is passed on. Comparing results between social and less social species might then in turn reveal if the degree of sociality has an effect on the type or degree of social information use, a previously completely unexplored research endeavour.

5. Avoidance of harmful invasive prey species

A single aversive event can prevent reptiles from consuming novel toxic invaders (e.g. Price-Rees et al., 2011; 2013; Somaweera et al., 2011; Ward-Fear et al., 2016; 2017) that can have detrimental effects on naïve native species (e.g. Indigo et al., 2018). Crocodiles (*C. johnstoni*), blue-tongue skinks (*T. scincoides*) and monitor lizards (*V. panoptes, V. rudicollis and V. varius*) can be trained to avoid toxic novel prey (cane toad, *R. marina*). Follow-up experiments could investigate if this behaviour is heritable (Kelly & Phillips, 2017; 2018) and/or if avoidance behaviour can be socially transmitted to naïve individuals. Previous work demonstrated information transmission through enhancement and facilitation (e.g. Davis & Burghardt, 2011; Perez-Cembranos & Perez-Mellado, 2015) even in wild reptiles (e.g. Schall, 2000). Conservation interventions will benefit from adopting a more behaviour-centred approach by incorporating species-specific cognitive abilities in avoidance learning and social information use. Previous work has already demonstrated that social learning is widespread among reptiles (see section III.9). Training a subset of individuals to spread valuable information (genetically or through social transmission) might prove effective and

relatively fast and cheap, helping conservation efforts.

6. Executive function

Core executive function comprise inhibitory skills, working memory, and flexibility in cognition. These processes prevent automatic responses allowing individuals to make informed decisions. Tests for executive function include reversal learning, set-shifting, or detour tasks which are well studied in mammals (Brown & Tait, 2015; Diamond, 2013) but less well in other vertebrates. In reptiles, behavioural flexibility has been investigated using reversal learning, however, how inhibition is exerted during reversals has received little attention. Furthermore, one lizard species demonstrated motor response inhibition in a detour reaching task (Szabo et al., 2019b) and one turtle (Cranney & Powers, 1983) and two lizard species (Szabo et al., 2018; 2019a) were able to perform an extradimensional shift in a set-shifting task, but if an attentional-set was formed could not be determined. Importantly, working memory has, so far, been unexplored in reptiles. Executive functions comprise layers of processing forming the basis of higher order abilities such as planning, reasoning and self-regulation (Diamond, 2013). To understand if reptiles do, for example, plan their actions we first need to establish if they possess basic executive function underlying these complex, higher-order abilities.

7. Spatial cognition in the context of sexual selection

Sex-specific differences in ecological demands and the resulting selective pressures can lead to adaptive specialisation, including in cognitive ability (Alcock, 1998). For example, the sexes differ in spatial memory ability in promiscuous mammals while not in monogamous species likely due to different selective pressures resulting from different spatial demands between males and females (Gaulin & Fitzgerald, 1989; Perdue et al., 2011). Most studies on spatial learning, especially in lizards, have tested only males (e.g. Day et al., 1999; 2001; Foa et al., 2009; LaDage et al., 2012; Mueller-Paul et al., 2012) and studies investigating

both sexes rarely considered sex during analyses (e.g. Lopez et al., 2000; 2001; Zuri & Bull, 2000). Only a single study *a priori* considered sex as a possible factor explaining individual variation in learning performance and subsequently uncovered a significant sex-based difference in spatial learning (Carazo et al., 2014). Sex-dependent spatial learning could be quite common given that males and females of many lizard species differ in home range size (Stamps, 1977). Differences in space use patterns can arise with increased sexual selection, when males defend territories or actively search for females (Cummings, 2018). It would be quite interesting to compare male and female spatial learning performance between species with high and low levels of sexual selection such as polygamous versus monogamous (respectively) lizards. Venturing into this unexplored research field will likely produce novel insights into reptile spatial navigation and how sexual selection shapes spatial learning.

V. Conclusions

(1) Our knowledge of reptile learning has greatly advanced, especially in the last decade. Most studies included here were conducted on lizards and turtles and little is known about learning abilities in snakes, the tuatara and crocodilians, a bias that has persisted since the emergence of the field. Although the range of species tested has expanded, our review still emphasises the need for the application of a broader taxonomic coverage within reptiles.

(2) We provide an up-to-date overview of the currently available knowledge on reptile learning and summarise the results of 118 studies showing how reptiles habituate behaviour, how they can be trained to perform new behaviour, how they avoid aversive stimuli including flavour aversion learning and escaping predators; which cues they use during spatial learning as well as foraging, their numerical abilities, their ability to learn novel foraging techniques, how they cope with change, and what we know about their social learning ability.

(3) We highlight seven contemporary research themes and avenues which we

1408 believe will be of special interest in the near future:

1409 • We still know little about how learning ability affects fitness in reptiles.
1410 Research into individual differences in cognitive abilities will help inform on
1411 selection pressures and consequently, evolutionary mechanisms.
1412 • Reptiles show a great range in ecology, life-history and behaviour. It is
1413 therefore important to consider these traits and tailor experiments to their
1414 specific ailities, to select appropriate model species as well as consider their
1415 specific need during experimental design.
1416 • Behaviour and learning might be important attributes for invasive species
1417 when invading a new environment. A comparison in a variety of tasks
1418 between invasive and non-invasive species can further our knowledge of
1419 what makes a successful invader.
1420 • Although most reptiles are considered less social, some species have
1421 evolved kin-based sociality. Testing these lizards' social learning ability could
1422 disentangle which cognitive abilities are affected by sociality.
1423 • Social learning of avoidance behaviour could be used to teach reptiles to
1424 avoid harmful invasive prey species by spreading this knowledge to naïve
1425 individuals.
1426 • Reasoning and planning are higher order processes which require executive
1427 function such as inhibition, attention and memory. These processes are badly
1428 understood in reptiles but could provide novel insights into the evolution of
1429 intelligence.
1430 • When ecological demands differ between the sexes, males and females
1431 might show different adaptive specialisations such as differences in spatial
1432 learning strategy and performance. This has been well studied in mammals
1433 and some birds and fishes but has largely been ignored in reptiles.

1434 (4) Our review shows that difference in cognitive ability between distantly related

taxa are not that of degree, but kind. Reptiles are not just driven by instinct but their abilities are certainly not those of higher primates. The field of reptile cognition has reached a point in which it will be important to move from descriptive studies testing if a species can learn a task towards a more experimental approach to elucidate the drivers of cognitive variation within and between species. This will ensure that the field will move forward and produce high quality research in the future. Furthermore, a more ecologically adapted approach will produce higher quality data better interpretable in relation to fitness. We want to encourage researchers to venture into this young and promising field and to be bolder in applying complex methodologies taking inspiration from other fields such as experimental and comparative psychology.

VI. Acknowledgements

Birgit Szabo was funded by an iMQRes scholarship during the writing of this paper, awarded by Macquarie University. We want to thank Gordon Burghardt and an anonymous reviewer for their very insightful and helpful comments provided during the review process.

VII. Supporting information

Due to the large number of studies our review focused on the main results. Further details on each study including task specifics, stimuli and reward used during testing, learning criteria as well as age and origin of animals are summarised in Table 1. All common and species names are based on Uetz et al., 2019.

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Table 1. Summary table presenting additional information not included in the main text. # - study number, learning task – details of the tested task (e.g. Spatial learning task with eight choices in an arena), stimulus and reward used and what learning criterion was applied. The table also includes the species tested, age-class of animals, their origin and the source (reference) of the data. Data is sorted by order, alphabetically by species name and date of publication. * in front of the species name indicates membership of Serpentes. Studies are highlighted alternating grey and white; rows indicate number of tests applied.

SAURIA											
#	**Learning task**			**Stimulus**	**Reward**	**Criterion**	**Species**	**Family**	**Age-class**	**Origin**	**Source**
1	Spatial	8-choice	Arena	Distal Cues Local Cue Light	Heat	No criterion, latency measured	Bosk's fringe-fingered lizard *(Acanthodactylus boskianus)*	Lacertidae	Adult	Wild	Day et al., 1999
	Discrimination	2-choice	Fork	Multiple	Food	10/12					
	Spatial	8-choice	Arena	Distal Cues Local Cue Light	Heat	No criterion, latency measured	Nidua fringe-fingered lizard *(Acanthodactylus scutellatus)*				
	Discrimination	2-choice	Fork	Multiple	Food	10/12					
2	Spatial	2-choice	Arena	Location	Shelter	No criterion	Lesueur's velvet gecko *(Amalosia lesueurii)*	Diplodactylidae	Hatchling	Captive	Dayananda & Webb, 2017
3	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, eaten or not	Green anole *(Anolis carolinensis)*	Dactyloidae	Adult	Captive	Stanger-Hall et al., 2001
4	Conditioning	1-choice	Run-way	Colour	Food	No criterion, proportion correct	Crested anole *(Anolis cristatellus)*	Dactyloidae	Adult/ Subadult	Wild	Shafir & Roughgarden, 1994
	Discrimination	2-choice	T-Maze								
5	Motor Task	1-choice	Wells	Multiple	Food	6/6	Crested anole *(Anolis cristatellus)*	Dactyloidae	Adult	Wild	Powell, 2012
	Discrimination	2-choice	Wells	Colour							
	Reversal	2-choice	Wells								
	Motor Task	1-choice	Wells	Multiple	Food	6/6	Emerald anole *(Anolis*				
	Discrimination	2-choice	Wells	Colour							

	Reversal	2-choice	Wells				*evermanni)*				
	Motor Task	1-choice	Wells	Multiple	Food	6/6	Puerto Rican anole *(Anolis pulchellus)*				
	Discrimination	2-choice	Wells	Colour							
	Reversal	2-choice	Wells								
6	Discrimination	2-choice	Wells	Colour	Food	6/6	Emerald anole *(Anolis evermanni)*	Dactyloidae	Adult	Wild	Leal & Powell, 2012
	Reversal	2-choice	Wells								
7	Conditioning	1-choice	Arena	Sound	Escape	No criterion, 80 trials	Graham's anole *(Anolis grahami)*	Dactyloidae	Adult	Not Given	Rothblum et al., 1979
8	Avoidance	1-choice	Box	Shock	Relieve	No criterion, number of shocks	Brown anole *(Anolis sagrei)*	Dactyloidae	Adult	Captive	Punzo, 1985
9	Spatial	4-choice	Arena	Local Cues	Heat	No criterion, latency measured	Little striped whiptail *(Aspidoscelis inornatus)*	Teiidae	Adult	Wild	Day et al., 2001
10	Spatial	2-choice	Arena	Multiple	Shelter	2x6/8	Little striped whiptail *(Aspidoscelis inornatus)*	Teiidae	Adult	Wild	Day et al., 2003
11	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Brown basilisk *(Basiliscus vittatus)*	Corytophanidae	Subadult	Not Given	Paradis & Cabanac, 2004
	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Common basilisk *(Basiliscus basiliscus)*				
	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Schneider's skink *(Eumeces schneideri)*	Scincidae			
	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, remaining food weighed	Common sun skink *(Eutropis multifasciata)*				
12	Spatial	2-choice	Arena	Location	Shelter	No criterion, 16 trials	Three-lined skink *(Bassiana*	Scincidae	Hatchling	Captive	Amiel & Shine, 2012

							duperreyi)				
13	Discrimination	2-choice	Y-Maze	Multiple	Food	No criterion, 15 trials	Three-lined skink *(Bassiana duperreyi)*	Scincidae	Hatchling	Captive	Amiel et al., 2014
14	Motor Task	1-choice	Wells	Multiple	Food	5/6	Three-lined skink *(Bassiana duperreyi)*	Scincidae	Hatchling	Captive	Clark et al., 2014
	Discrimination	3-choice	Wells								
	Discrimination	3-choice	Wells	Colour							
	Reversal	3-choice	Wells								
15	Discrimination	2-choice	Arena	Colour	Food	No criterion, number consumes	Oriental garden lizards (*Calotes versicolor)*	Agamidae	Hatchling	Captive	Shanbhag et al., 2010
16	Discrimination	n-choice	Natural habitat	Colour	Food	No criterion, volume and damage recorded	Laurent's whiptail *(Cnemidophorus murinus)*	Teiidae	Adult	Wild	Schall, 2000
	Discrimination	n-choice	Natural habitat	Location							
17	Spatial	2-choice	Y-Maze	Position	Food	16/20	Western banded gecko *(Coleonyx variegatus)*	Eublepharidae	Adult	Not Given	Kirkish et al., 1979
	Reversal	2-choice	Y-Maze								
18	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, latency measured	Jamaican iguana *(Cyclura collei)*	Iguanidae	Adult	Captive	Cooper et al., 2019
	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, latency measured	Beaded lizard *(Heloderma charlesbogerti)*	Helodermatidae	Adult/ subadult		
	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, latency measured	Mertens's Water Monitor *(Varanus mertensi)*	Varanidae	Adult		
	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, latency measured	Roughneck monitor *(Varanus rudicollis)*		Adult		
	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, latency measured	Emerald monitor *(Varanus prasinus)*		Adult		
19	Conditioning	-	Arena	Clicker	Food	Not given	Caiman lizard *(Dracaena guianensis)*	Teiidae	Subadult/ adult	Captive	Hellmuth et al., 2012
	Conditioning	1-chocie	Arena	Target							
20	Spatial	3-choice	Vertical	Multiple	Food	5/6	Tree skink	Scincidae	Juvenile	Captive	Riley et al., 2016

			Maze				*(Egernia striolata)*				
21	Motor Task	1-choice	Wells	Multiple	Food	5/6	Tree skink *(Egernia striolata)*	Scincidae	Juvenile	Captive	Riley et al., 2018
	Social	Discrimi-nation	Wells	Multiple	Food	7/8					
	Social	Reversal	Wells								
22	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Tree skink *(Egernia striolata)*	Scincidae	Adult	Wild	Szabo et al., 2018
	Reversal	2-choice	Wells								
23	Discrimination	2-choice	Wells	Colour	Food	7/8	Tree skink *(Egernia striolata)*	Scincidae	Adult	Wild	Whiting et al., 2018
24	Spatial	2-choice	Arena	Location	Shelter	No criterion, 16 trials	Mongolia racerunner *(Eremias argus)*	Lacertidae	Hatchling	Captive	Sun et al., 2014
25	Spatial	3-choice	Arena	Location	Shelter	5/5	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Noble et al., 2012
	Reversal	3-choice	Arena								
26	Spatial	2-choice	Arena	Location	Shelter	Significant performance	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Carazo et al., 2014
27	Motor Task	1-choice	Wells	Multiple	Food	5/6	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Noble et al., 2014
	Discrimination	2-choice	Wells								
	Social	2-choice	Wells								
28	Social	Discrimi-nation	Wells	Multiple	Food	5/6	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Kar et al., 2017
	Social	Reversal	Wells								
29	Motor Task	1-choice	Wells	Multiple	Food	5/6	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Qi et al., 2018
	Discrimination	3-choice	Wells	Multiple							
	Discrimination	3-choice	Wells	Colour							
30	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Eastern water skink *(Eulamprus quoyii)*	Scincidae	Adult	Wild	Szabo et al., 2019b
	Detour	1-choice	Cylinder	Multiple	Food	4/5					
	Detour	1-choice	Cylinder	Multiple	Food	correct out of 10					
31	Discrimination	2-choice	Y-Maze	Multiple	Food	No criterion, 15 trials	Delicate skink *(Lampropholis delicata)*	Scincidae	Adult	Wild	Bezzina et al., 2014
	Discrimination	2-choice	Y-Maze	Multiple	Food	No criterion, 15 trials	Common garden skinks				

							(Lampropholis guichenoti)				
32	Spatial	2-choice	Arena	Location	Shelter	5/6	Delicate skink *(Lampropholis delicata)*	Scincidae	Adult	Wild	Chung et al., 2017
33	Discrimination	2-choice	Y-Maze	Multiple	Shelter	5/6	Delicate skink *(Lampropholis delicata)*	Scincidae	Adult	Wild	Kang et al., 2018
	Discrimination	2-choice	Y-Maze	Colour							
34	Discrimination	2-choice	Y-Maze	Multiple	Shelter	5/6	Delicate skink *(Lampropholis delicata)*	Scincidae	Adult	Wild	Goulet et al., 2018
	Discrimination	2-choice	Y-Maze	Colour							
35	Avoidance	n-choice	Natural Habitat	Threat	Shelter	Defence reaction	Red-sided curlytail *(Leiocephalus schreibersii)*	Leiocephalidae	Adult	Wild	Marcellini & Jenssen, 1991
36	Social	Discrimi-nation	Wells	Multiple	Food	7/8	White's skink *(Liopholis whitii)*	Scincidae	Adult	Wild	Munch et al., 2018
	Social	Reversal	Wells								
37	Discrimination	2-choice	Wells	Multiple	Food	No criterion, 20 trials	White's skink *(Liopholis whitii)*	Scincidae	Juvenile	Captive	Munch et al., 2018
	Spatial	2-choice	Arena	Location	Shelter						
38	Habituation	-	Arena	Threat	Shelter	No criterion, 6 test days	Iberian wall lizard *(Podarcis hispanicus)*	Lacertidae	Adult	Wild	Rodriguez-Priet et al., 2011
39	Social	Enhance-ment	Arena	Multiple	Food	No criterion, number of individuals	Lilford's wall lizard *(Podarcis lilfordi)*	Lacertidae	Adult	Wild	Perez-Cembranos & Perez-Mellado, 2015
	Social	Enhance-ment	Arena	Multiple	Conspe-cifics						
	Social	Enhance-ment	Arena	Multiple	Models						
40	Spatial	1-choice	Water Maze	Location	Escape	>6 for two sessions	Italian wall lizard *(Podarcis sicula)*	Lacertidae	Adult	Wild	Foa et al., 2009
41	Discrimination	2-choice	Y-Maze	Quantity	Food	75% correct 2 days, >chance 120 trials	Italian wall lizard *(Podarcis sicula)*	Lacertidae	Adult	Wild	Petrazzini et al., 2018
	Discrimination	2-choice	Y-Maze	Size							
42	Motor Task	1-choice	Wells	Multiple	Food	7/7 or 7/8	Italian wall lizard	Lacertidae	Adult	Wild	Damas-Moreira et

	Discrimination	3-choice	Wells	Colour			*(Podarcis sicula)*				al., 2018
	Social	3-choice	Wells								
43	Discrimination	2-chocie	Y-Maze	Quantity	Food	No criterion, 64 trials	Italian wall lizard *(Podarcis sicula)*	Lacertidae	Adult	Wild	Petrazzini et al., 2017
	Discrimination	2-chocie	Y-Maze	Size							
44	Social	Bidirecti-onal	Door	Direction	Food	No criterion, 10 trials	Central bearded dragon *(Pogona vitticeps)*	Agamidae	Adult	Captive	Kis et al., 2015
45	Social	Bidirec-tional	Door	Direction	Food	No criterion, 10 trials	Central bearded dragon *(Pogona vitticeps)*	Agamidae	Adult	Captive	Siviter et al., 2017
46	Discrimination	2-choice	Arena	Location	Shelter	5/5	South Indian rock agama *(Psammophilus dorsalis)*	Agamidae	Adult	Wild	Batabyal & Thaker, 2019
	Reversal	2-choice	Arena								
47	Discrimination	2-choice	Arena	Shape	Food	Minimum 5/6	European glass lizard *(Pseudopus apodus)*	Anguidae	Adult	Wild	Ivazov, 1983
48	Spatial	4-choice	Arena	Location	Food	No criterion	Crevice spiny lizard *(Sceloporus poinsettii)*	Phrynosoma-tidae	Adult	Captive	Punzo, 2002
49	Avoidance	n-choice	Natural Habitat	Threat	Shelter	No criterion, hiding time and FID	Fence lizard *(Sceloporus undulatus)*	Phrynosoma-tidae	Adult	Wild	Thaker et al., 2010
50	Taste Aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard *(Sceloporus undulatus)*	Phrynosoma-tidae	Juvenile	Wild	Robbins et al., 2013
51	Taste Aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard *(Sceloporus undulatus)*	Phrynosoma-tidae	Sub-adult	Wild	Herr et al., 2016
52	Taste Aversion	2-choice	Arena	Venom	Food	No criterion	Fence lizard *(Sceloporus undulatus)*	Phrynosoma-tidae	Hatchling	Captive	Venable et al., 2019
53	Spatial	2-choice	Arena	Location	Shelter	No criterion, latency measured	Little brown skink *(Scincella lateralis)*	Scincidae	Adult	Wild	Paulissen, 2008
	Spatial	2-choice	Arena	Location + Experience							
54	Discrimination	2-choice	Arena	Pattern	Shelter	5/5	Little brown skink *(Scincella*	Scincidae	Adult	Wild	Paulissen, 2014

							lateralis)				
55	Discrimination	2-choice	Arena	Multiple	Shelter	No criterion, time at location	Sleepy lizard *(Tiliqua rugosa)*	Scincidae	Adult	Wild	Zuri & Bull, 2000
56	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, remaining food	Eastern blue-tongue skink *(Tiliqua scincoides)*	Scincidae	Adult/ Subadult	Mixed	Price-Rees et al., 2011
57	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, vomiting	Eastern blue-tongue skink *(Tiliqua scincoides)*	Scincidae	Adult	Wild	Price-Rees et al., 2013
58	Discrimination	2-choice	Wells	Multiple	Food	6/6 or 7/8	Eastern blue-tongue skink *(Tiliqua scincoides)*	Scincidae	Adult/ Juveniles	Wild	Szabo et al., 2019a
	Reversal	2-choice	Wells								
59	Spatial	8-choice	Radial Arm Maze	Location	Food	40 trial 6/18 correct in last 20 trials	Jewelled lizard *(Timon lepidus)*	Lacertidae	Adult/ Subadult	Captive	Mueller-Paul et al., 2012
60	Avoidance	1-choice	Shuttle Box	Light	Relieve	Mean % avoidance	Common golden tegu *(Tupinambis teguixin)*	Teiidae	Juvenile	Not Given	Yori, 1978
61	Spatial	10-choices	Barnes Maze	Location	Shelter	3/3	Side-blotched lizard *(Uta stansburiana)*	Phrynosoma-tidae	Subadult	Captive	LaDage et al., 2012
62	Problem Solving	1-choice	Puzzle Box	Visual	Food	No criterion, 3 trials	White-throated monitor *(Varanus albigularis)*	Varanidae	Juvenile	Captive	Manrod et al., 2008
63	Discrimination	2-choice	Target	Brightness	Food	2x8/10	Komodo dragon *(Varanus komodoensis)*	Varanidae	Adult	Captive	Gaalema, 2007
	Reversal	2-choice	Target								
	Reversal	2-choice	Target								
64	Taste Aversion	1-choice	Natural Habitat	Taste	Food	No criterion, biting of toad	Yellow-spotted monitor *(Varanus panoptes)*	Varanidae	Adult	Wild	Ward-Fear et al., 2016
65	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, interest levels	Yellow-spotted monitor *(Varanus panoptes)*	Varanidae	Adult	Wild	Ward-Fear et al., 2017

66	Taste Aversion	2-choice	Natural Habitat	Taste	Food	No criterion, eaten or not	Yellow-spotted monitor *(Varanus panoptes)*	Varanidae	Mixed	Wild	Llewelyn et al., 2014
	Taste Aversion	2-choice	Natural Habitat	Taste	Food	No criterion, eaten or not		Varanidae	Adult		
67	Discrimination	2-choice	Target	Brightness	Food	2x8/10	Roughneck monitor *(Varanus rudicollis)*	Varanidae	Adult	Not Given	Gaalema, 2011
	Reversal	2-choice	Target								
	Reversal	2-choice	Target								
68	Taste Aversion	3-choice	Natural Habitat	Taste	Food	No criterion, eaten or not	Lace monitor *(Varanus varius)*	Varanidae	Mixed	Wild	Jolly et al., 2016
	Taste Aversion	3-choice	Natural Habitat	Taste	Food	No criterion, eaten or not					
	Taste Aversion	3-choice	Natural Habitat	Taste	Food	No criterion, eaten or not					
SERPENTES											
#	**Learning task**			**Stimuli**	**Reward**	**Criterion**	**Species**	**Family**	**Age-class**	**Origin**	**Source**
69	Habituation	-	Arena	Artificial human hand	None	No criterion, 5 days	Cottonmouth *(Agkistrodon piscivorus)*	Viperidae	Adult	Wild	Glaudas, 2004
70	Habituation	-	Arena	Artificial human hand	None	No criterion, 5 days	Cottonmouth *(Agkistrodon piscivorus)*	Viperidae	Adult	Wild	Glaudas et al., 2006
									Neonate	Captive	
71	Spatial	4-choice	Arena	White card	Shelter	No criterion, 16 trials	Cottonmouth *(Agkistrodon piscivorus)*	Viperidae	Juvenile	Captive	Friesen, 2017
	Discrimination	2-choice	Arena	Red card	Food	No criterion, 11-14 days					
72	Spatial	8-choice	Arena	Multiple	Shelter	8/10	Spotted python *(Antaresia maculosa)*	Pythonidae	Juvenile	Captive	Stone et al., 2000
73	Habituation	-	Box	Lid opening	None	No response in 10/10 or 120 trials max	Diamondback rattlesnakes (*Crotalus atrox)*	Viperidae	Adult	Wild	Place & Abramson, 2008
74	Conditioning	1-choice	Arena	Target	Food	Not given	False water cobra *(Hydrodynastes gigas)*	Colubridae	Juvenile	Not given	Data presented by Hellmuth et al., 2012

75	Conditioning	1-choice	Key	Light	Food	No criterion, 20 trials	Montpellier snake (*Malpolon monspessulanus*)	Psammophiidae	Not Given	Not Given	Gavish, 1979
76	Spatial	4-choice	Arena	Location	Shelter	No criterion, latency measured	Red cornsnake *(Pantherophis guttatus)*	Colubridae	Adult	Not Given	Holtzman, 1995
77	Spatial	8-choice	Arena	Location	Shelter	No criterion, latency measured	Red cornsnake *(Pantherophis guttatus)*	Colubridae	Juvenile	Captive	Holtzman et al., 1999
78	Spatial	12-choice	Arena	Location	Shelter	No criterion, latency measured	Rat snake *(Pantherophis obsoletus)*	Colubridae	Juvenile	Captive	Almli & Burghardt, 2006
79	Conditioning	1-choice	Key	Light	Food	No criterion, latency measured	Indian rock python *(Python molurus)*	Pythonidae	Neonatal	Mixed	Emer et al., 2015
80	Habituation	-	Arena	Human hand	None	No criterion, one 60 sec presentation	Butler's garter snake (*Thamnophis butleri*)	Colubridae	Neonatal	Captive	Herzog et al., 1989
	Habituation	-	Arena	Human hand	None	No criterion, one 60 sec presentation, repeated	Mexican garter snake (*Thamnophis melanogaster*)				
	Habituation	-	Arena	Human hand	None	No criterion, 10 presentations in 30 sec	Mexican garter snake (*Thamnophis melanogaster*)	Colubridae	Juvenile		
81	Discrimination	2-choice	Arena	Lemon odour	Food	No criterion, 100 trials	Plains garter snake (*Thamnophis radix*)	Colubridae	Juvenile/ adult	Captive	Begun et al., 1988
	Reversal	2-choice	Arena	Pine odour	Food	No criterion, 50 trials					
	Discrimination	2-choice	Y-maze	Amyl acetate	Food	Cumulative correct above chance in 2 sessions			Adult		
82	Taste Aversion	1-choice	Arena	Multiple	Food	No criterion, attack	Plains garter snake	Colubridae	Adult	Captive	Terrick et al., 1995
	Taste Aversion	2-choice	Arena								

	Taste Aversion	2-choice	Arena			latency	(*Thamnophis radix*)				
83	Habituation	-	Arena	Grey card	None	No response in 4/4	Common garter snake *(Thamnophis sirtalis)*	Colubridae	Neonate	Captive	Hampton & Gillingham, 1989
	Habituation	-	Arena	Grey card	None	No response in 4/4, for 5 days					
RHYNCHOCEPHALIA											
#	**Learning task**			**Stimuli**	**Reward**	**Criterion**	**Species**	**Family**	**Age-class**	**Origin**	**Source**
84	Discrimination	2-choice	Arena	Frequency	Food	No criterion	Tuatara *(Sphenodon punctatus)*	Sphenodontidae	Juvenile	Captive	Woo et al., 2009
CHELONIA											
#	**Learning task**			**Stimuli**	**Reward**	**Criterion**	**Species**	**Family**	**Age-class**	**Origin**	**Source**
85	Conditioning	-	Arena	Whistle	Food	Food search after sound	Aldabra tortoises (*Aldabrachelys gigantea*)	Testudinidae	Adult	Captive	Weiss & Wilson, 2003
	Conditioning	1-choice	Arena	Red target	Food	Reliably touching target					
86	Conditioning	1-choice	Arena	Blue-and-white target	Food	4x 30 sec holding	Aldabra tortoises (*Aldabrachelys gigantea*)	Testudinidae	Adult	Captive	Gaalema & Benboe, 2008
87	Spatial	8-choice	Radial Arm Maze	Location	Food	No criterion, number correct	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Adult	Captive	Wilkinson et al., 2007
88	Spatial	8-choice	Radial Arm Maze	Location	Food	No criterion, number correct	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Adult	Captive	Wilkinson et al., 2009
89	Social	Detour	Arena	Multiple	Food	No criterion, goal reached	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Juvenile/ Subadult	Not Given	Wilkinson et al., 2010
90	Social	Detour	Arena	Multiple	Food	No criterion,	Red-footed	Testudinidae	Juvenile/	Not Given	Wilkinson & Huber,

					goal reached	tortoise *(Chelonoidis carbonaria)*		Subadult		2012
91	Discrimination	2-choice	Arena	Visual	Food	No criterion, number correct	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Subadult	Captive	Wilkinson et al., 2013
92	Discrimination	2-choice	Touch Screen	Position	Food	Last 3 blocks above chance	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Juvenile	Captive	Mueller-Paul et al., 2014
	Discrimination	2-choice	Arena	Position	Food	No criterion, 20 trials					
	Reversal	2-choice	Touch Screen	Position	Food	Last 3 blocks above chance					
	Reversal	2-choice	Arena	Position	Food	No criterion, 20 trials					
93	Discrimination	2-choice	Arena	Quantity	Food	no criterion	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Subadult	Captive	Soldati et al., 2017
94	Discrimination	2-choice	Y-Maze	Multiple	Food	80% across 2 sessions	Red-footed tortoise *(Chelonoidis carbonaria)*	Testudinidae	Adult	Captive	Bridgeman & Tattersall, 2019
	Reversal	2-choice	Y-Maze								
95	Conditioning	1-choice	Arena	Neck touch	Food	No criterion	Galápagos tortoise (*Chelonoidis nigra*)	Testudinidae	Adult	Captive	Bryant et al., 2016
96	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Reiner & Powers, 1978
	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
97	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle *(Chrysemys picta)*	Emydidae	Not Given	Not Given	Reiner & Powers, 1980

	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
98	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Cranney & Powers, 1983
	Discrimination	2-choice	Keys	Multiple	Food	17/20					
	Reversal	2-choice	Keys								
	ED Shifts	2-choice	Keys								
99	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Reiner & Powers, 1983
	Discrimination	2-choice	Keys	Intensity	Food	80% 2 days					
	Discrimination	2-choice	Keys	Pattern	Food	90% 2 days					
100	Conditioning	1-choice	Key	Red light	Food	Short latencies for 3 days	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Grisham & Powers, 1989
	Discrimination	2-choice	Keys	Pattern	Food	Mean latency difference of 48s for 4 days					
101	Conditioning	1-choice	Key	Red light	Food	No criterion, fixed number of sessions	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Blau & Powers, 1989
	Discrimination	2-choice	Keys	Pattern	Food	17/20					
102	Conditioning	1-choice	Key	Red light	Food	Short latencies for 3 days	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Grisham & Powers, 1990
	Discrimination	2-choice	Keys	Position	Food	2x17/20					
	Reversal	2-choice	Keys								
103	Spatial	3-choice	X-Maze	Location	Water	67% 2 days	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Petrillo et al., 1994
104	Discrimination	2-choice	T-Maze	Position	Food	2/3 for 2 days	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Avigan & Powers, 1995
	Discrimination	2-choice	X-Maze								
105	Conditioning	1-choice	Keys	Red/white stripes	Food	No criterion, 18 days	Painted turtle *(Chrysemys picta)*	Emydidae	Adult	Not Given	Yeh & Powers, 2005

	Discrimination	3-choice	Keys	Multiple	Food	Probability of response					
106	Conditioning	1-choice	Keys	Red/white stripes	Food	No criterion, 18 days	Painted turtle *(Chrysemys picta)*	Emydidae	Subadult	Not Given	Powers et a., 2009
	Discrimination	2-choice	Keys	Multiple	Food	No criterion, responses per day					
	Negative Patterning	3-choice	Keys								
107	Spatial	n-choice	Natural Habitat	Multiple	None	No criterion	Painted turtle *(Chrysemys picta)*	Emydidae	Adults/ Juveniles	Mixed	Roth & Krochmal, 2015
	Discrimination	2-choice	Y-Maze	UV Odour	None	No criterion, proportion correct					
108	Conditioning	1-choice	Runway	Quantity	Food	No criterion, latency measured	Reeves' turtle *(Mauremys reevesii)*	Geoemydidae	Adult	Not Given	Papini & Ishida, 1994
109	Conditioning	1-choice	Runway	Location	Food	No criterion, latency measured	Reeves' turtle *(Mauremys reevesii)*	Geoemydidae	Adult	Not Given	Ishida & Papini, 1997
110	Discrimination	2-choice	Bottles	Visual	Food	No criterion, latency measured	Florida red-bellied cooter *(Pseudemys nelsoni)*	Emydidae	Adult	Captive	Davis & Burghardt, 2007
111	Social	Discrimi-nation	Bottles	Brightness	Food	6/6	Florida red-bellied cooter *(Pseudemys nelsoni)*	Emydidae	Adult	Captive	Davis & Burghardt, 2011
112	Discrimination	2-choice	Bottles	Food Pellet	Food	6/6	Florida red-bellied cooter *(Pseudemys nelsoni)*	Emydidae	Adult	Captive	Davis & Burghardt, 2012
	Discrimination	2-choice	Bottles	Brightness							
	Discrimination	2-choice	Bottles	Brightness	Food	6/6	Pond slider *(Trachemys scripta)*				
113	Discrimination	2-choice	Target	Brightness			Box turtle *(Terrapene carolina)*	Emydidae	Adult	Captive	Leighty et al., 2013
	Discrimination	2-choice	Target	Brightness	Food	11/12 for 5 sessions					
	Discrimination	2-choice	Target	Brightness	Food	No criterion					
	Discrimination	2-choice	Target	Brightness	Food	9/10 for					

					5 sessions					
114	Discrimination	2-choice	Y-Maze	Quantity	Food	No criterion, 60 trials	Hermann's tortoise *(Testudo hermanni)*	Testudinidae	Adult	Wild	Gazzola et al., 2018
	Discrimination	2-choice	Y-Maze	Size							
115	Spatial	4-choice	4-Arm Maze	Distal Cues Local Cue	Food	13/15	Pond slider *(Trachemys scripta)*	Emydidae	Juvenile	Not Given	Lopez et al., 2000
116	Spatial	4-choice	Water Maze	Distal Cues Local Cue	Food	9/18	Pond slider *(Trachemys scripta)*	Emydidae	Subadult	Not Given	Lopez et al., 2001
CROCODILIA											
#	**Learning task**			**Stimuli**	**Reward**	**Criterion**	**Species**	**Family**	**Age-class**	**Origin**	**Source**
117	Conditioning	-	Arena	Clicker	Food	Food search after sound	Nile crocodile *(Crocodylus niloticus)*	Crocodylidae	Subadult	Not Given	Augustine & Baumer, 2012
	Conditioning	1-choice	Arena	Black target	Food	Reliably touching target					
118	Taste Aversion	1-choice	Arena	Taste	Food	No criterion, eaten or not	Freshwater crocodile *(Crocodylus johnstoni)*	Crocodylidae	Juvenile	Wild	Somaweera et al., 2011

Figures

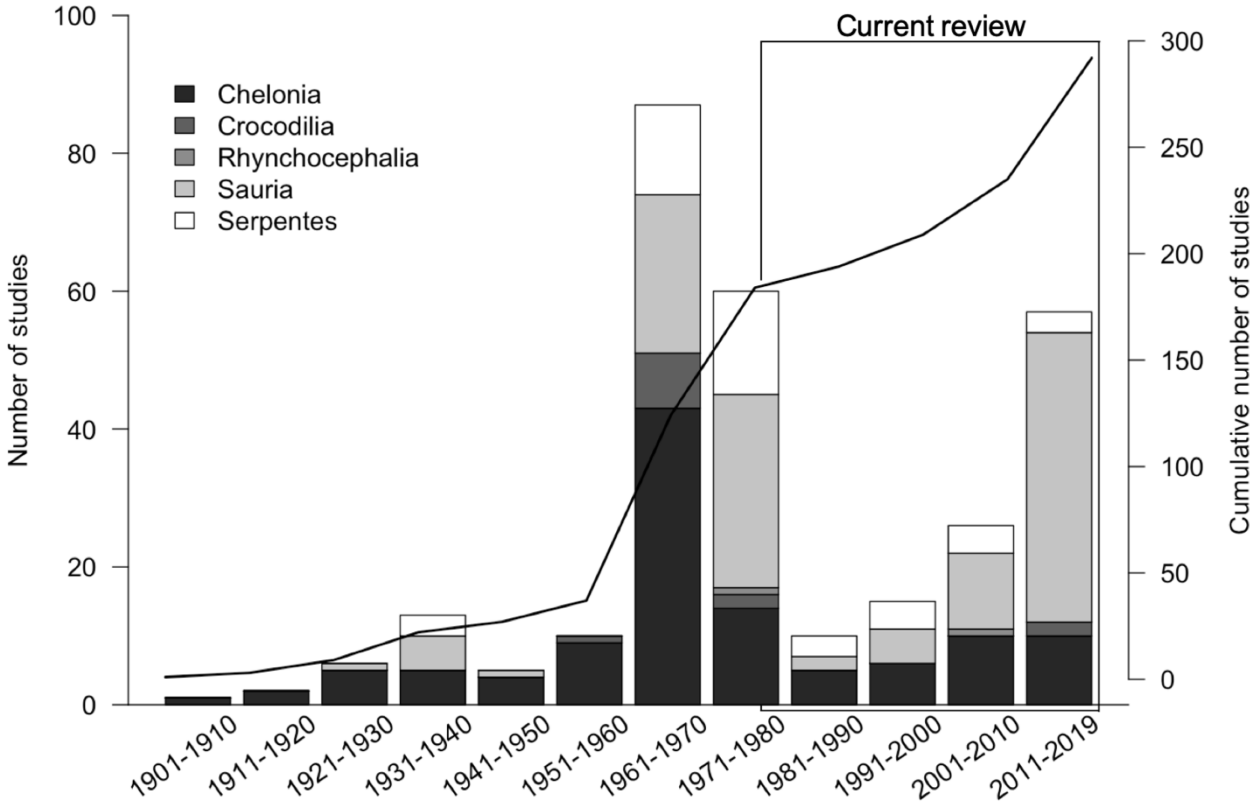

Figure 1. Bar chart: Number of studies from before 1901 to 2019 (in 10-year intervals) split between the main orders of reptiles; Squamates are split into Sauria (lizards) and Serpentes (snakes). Superimposed as a line is the cumulative number of studies. Only studies conducted after 1977 and not included in Burghardt (1977) are included in this review.

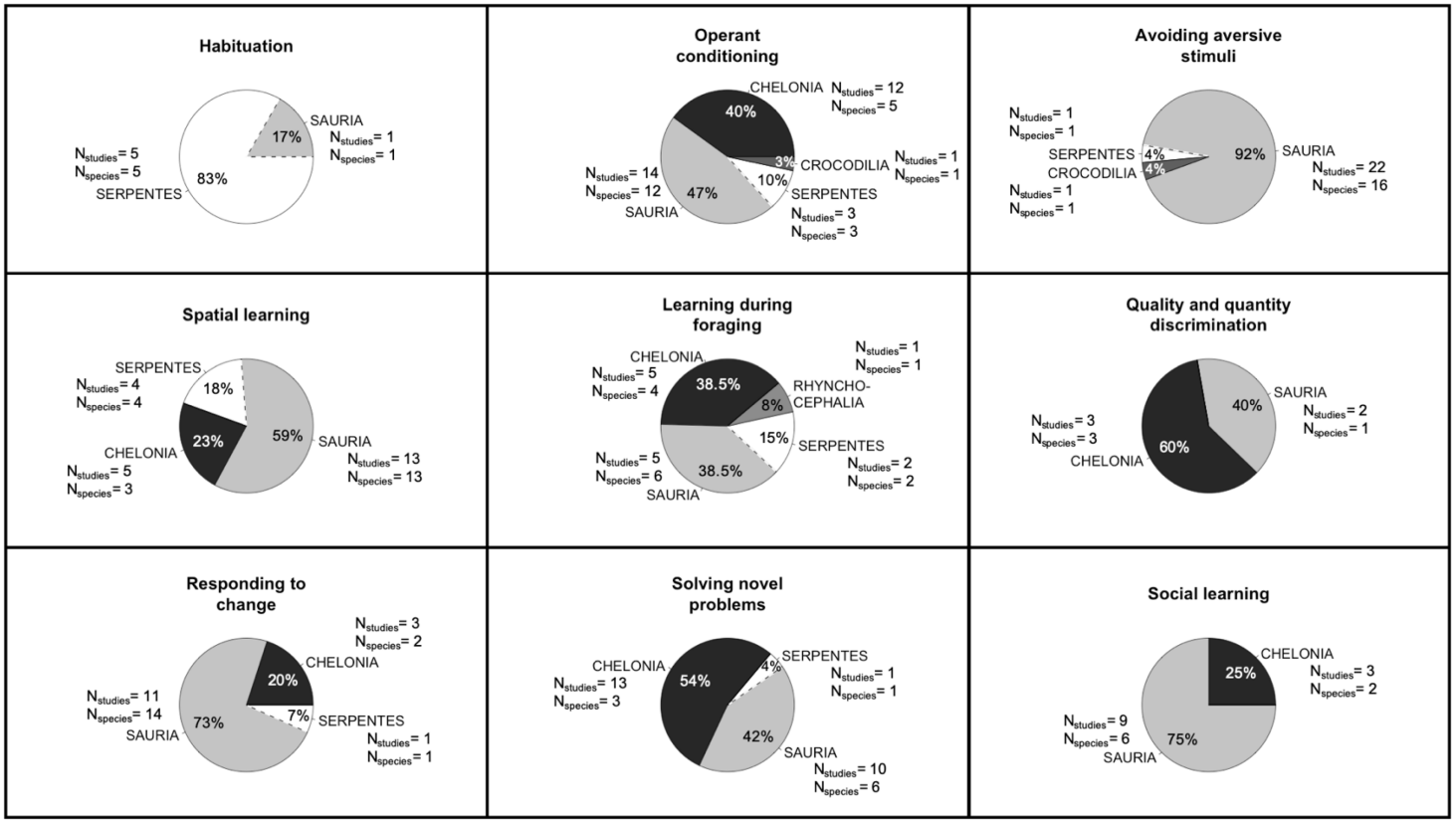

Figure 2. Pie charts summarising the proportion (in % of studies) of taxa tested in the last 40 years since Burghardt (1977) on a learning ability consolidated under one of nine umbrella terms used in this systematic review. The chart headings correspond to the subsection headings in the review text. Black – turtles and tortoises (Chelonia), dark grey – crocodiles (Crocodilia), medium grey – tuatara (Rhynchocephalian), light grey – lizards (Sauria) and white – snakes (Serpents). The dashed line separating lizards and snakes indicates that both belong to Squamates. Next to each taxon we present the number of studies and number of species included in our review.

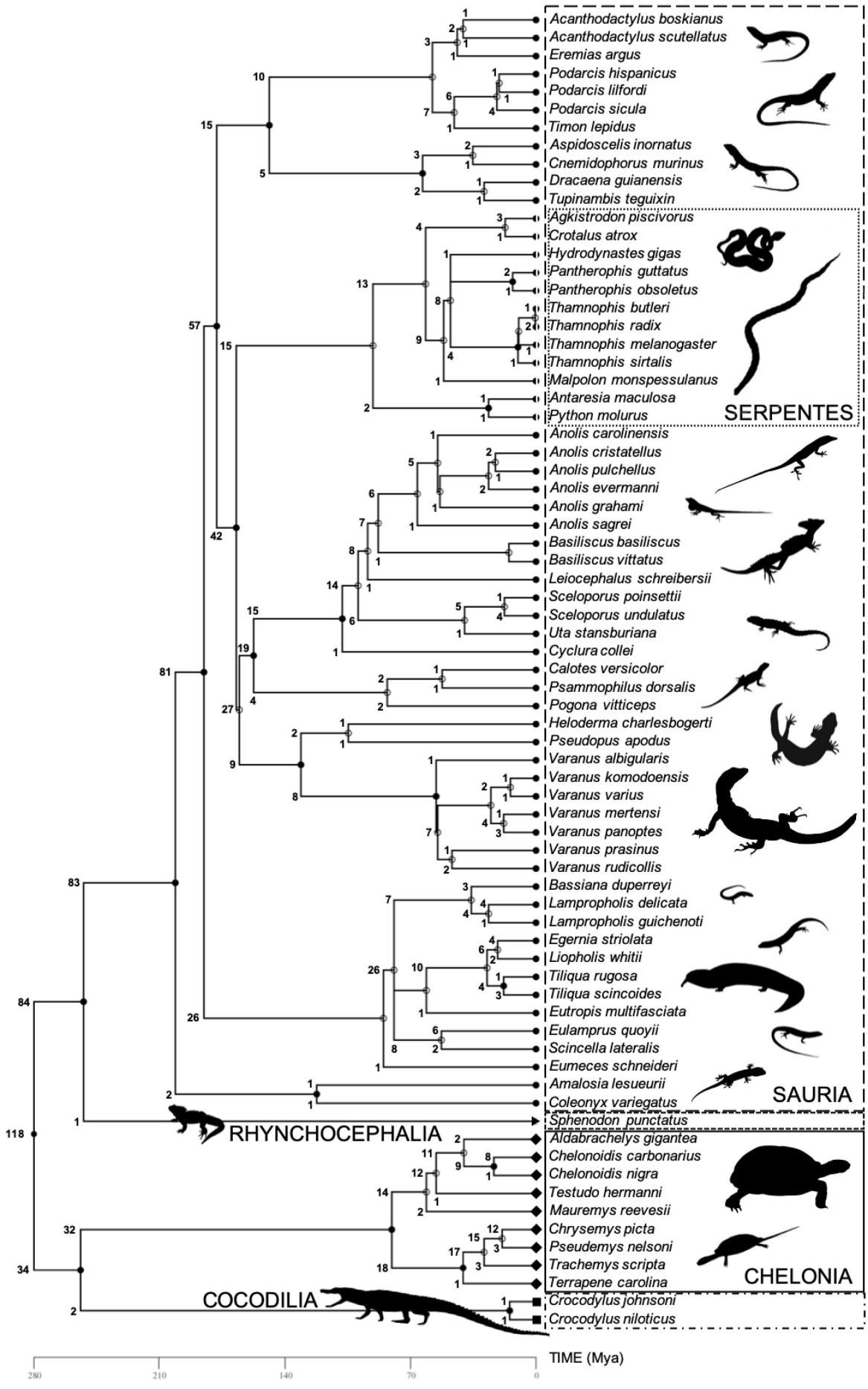
Acanthodactylus boskianus
Acanthodactylus scutellatus
Eremias argus
Podarcis hispanicus
Podarcis lilfordi
Podarcis sicula
Timon lepidus
Aspidoscelis inornatus
Cnemidophorus murinus
Dracaena guianensis
Tupinambis teguixin
Agkistrodon piscivorus
Crotalus atrox
Hydrodynastes gigas
Pantherophis guttatus
Pantherophis obsoletus
Thamnophis butleri
Thamnophis radix
Thamnophis melanogaster
Thamnophis sirtalis
Malpolon monspessulanus
Antaresia maculosa
Python molurus
SERPENTES
Anolis carolinensis
Anolis cristatellus
Anolis pulchellus
Anolis evermanni
Anolis grahami
Anolis sagrei
Basiliscus basiliscus
Basiliscus vittatus
Leiocephalus schreibersii
Sceloporus poinsettii
Sceloporus undulatus
Uta stansburiana
Cyclura collei
Calotes versicolor
Psammophilus dorsalis
Pogona vitticeps
Heloderma charlesbogerti
Pseudopus apodus
Varanus albigularis
Varanus komodoensis
Varanus varius
Varanus mertensi
Varanus panoptes
Varanus prasinus
Varanus rudicollis
Bassiana duperreyi
Lampropholis delicata
Lampropholis guichenoti
Egernia striolata
Liopholis whitii
Tiliqua rugosa
Tiliqua scincoides
Eutropis multifasciata
Eulamprus quoyii
Scincella lateralis
Eumeces schneideri
Amalosia lesueurii
Coleonyx variegatus
SAURIA
Sphenodon punctatus
RHYNCHOCEPHALIA
Aldabrachelys gigantea
Chelonoidis carbonarius
Chelonoidis nigra
Testudo hermanni
Mauremys reevesii
Chrysemys picta
Pseudemys nelsoni
Trachemys scripta
Terrapene carolina
CHELONIA
COCODILIA
Crocodylus johnsoni
Crocodylus niloticus
TIME (Mya)
280
210
140
70
0

Figure 3. The phylogenetic tree depicts our current understanding of the relationships among taxa included in our review split into Sauria, Serpentes (which together form Squamata), Rhynchocephalia, Chelonia and Cocodilia. Numbers at node splits represent the number of studies (some studies include multiple species). The tree was generated with http://timetree.org (Kumar et al., 2017). Animal outlines from http://www.phylopic.org/; picture copyright: turtle & caiman - Scott Hartman; tortoise - Andrew A. Farke; anole - Sarah Werning; https://creativecommons.org/licenses/by-nc-sa/3.0/